

CA1 IA 77A61

Canada, DINA.

ALUR 75-76-61

FIRE AND VEGETATION CHANGE IN THE WESTERN SUBARCTIC.
1977.

North of 60

Fire and Vegetation Change in the Western Subarctic

CA1 IA77 A61



Earth Sciences Library



Digitized by the Internet Archive
in 2025 with funding from
University of Toronto

<https://archive.org/details/31761056887938>

ALUR 1975-76

**Fire and Vegetation
Change in the
Western Subarctic**

E. A. Johnson
J. S. Rowe
Department of Plant Ecology
University of Saskatchewan

Published under authority of the
Hon. Warren Allmand,
Minister of Indian and Northern Affairs
Ottawa, 1977
QS-8138-000-EE-A1

©Minister of Supply and Services Canada 1977
Catalogue No. R71-18/76-1
ISBN 0-662-00765-4

This report was prepared under contract for the Arctic Land Use Research Program, Northern Natural Resources and Environment Branch, Department of Indian Affairs and Northern Development. The views, conclusions and recommendations expressed herein are those of the authors and not necessarily those of the Department.

ALUR 75-76-61

TABLE OF CONTENTS

LIST OF TABLES	(iii)
LIST OF FIGURES	(iv)
LIST OF PHOTOS	(vi)
ACKNOWLEDGEMENTS	1
 1. INTRODUCTION	 3
1.1 Physiography and Glaciation	3
1.2 Climate	6
1.3 Vegetation	7
1.4 Fire	7
 2. FIRE FREQUENCIES IN CARIBOU RANGE	 10
2.1 Methods	10
2.2 Discussion	12
2.3 Implications	15
2.4 Management Uses	18
 3. VEGETATION COMPOSITIONAL CHANGE	 23
3.1 Present state of knowledge	23
3.2 Field and Laboratory Methods	25
3.3 Methods of Analysis	29
3.4 Interpretation of Gradients	30
3.4.1 Heat Regime Gradient	30
3.4.2 Nutrient Regime Gradient	37
3.5 Change ("time") ordinations	37
3.6 Species Change	42
3.7 Community Change	49
3.8 Discussion	51
 4. REFERENCES	 53

LIST OF TABLES

Table

1.1	Summary of Forest Fires in the Caribou Range 1966-1975.	8
2.1	Location and information on regions sampled in fire frequency studies.	11
2.2	Fire frequency Weibull Parameter estimates using the method of D'Agostino (1971).	13
3.1	Suggested Heat Regime along Gradient I	35

LIST OF FIGURES

Figure

1.1	Map showing location of Caribou Range, N.W.T.	4
1.2	Map of landforms in Caribou Range.	5
2.1	Changes in Canadian Fire Weather Index (FWI) as calculated from meteorological parameters (from Simard 1974).	14
2.2	Relationship of distance from tree line and expected fire recurrence for region.	16
2.3	The relationship of vector dispersion (Terrain Roughness) and Weibull shape parameter.	17
3.1	Proposed successional sequences by respective authors.	24
3.2	Map showing the general location of the 141 stands sampled.	26
3.3	The frequency distribution of stand ages in this study.	28
3.4	The principal components ordination of species in which the variation due to age of stands has been removed.	31 32
3.5	Principal components ordination of stands in which the variation due to age of stands has been removed.	33
3.6	The average potential direct shortwave radiation (June equinox) (top) and average % canopy cover (bottom).	34
3.7	The average slope position on gradient I.	36
3.8	Changes in substrate characteristics across the nutrient regime gradient.	38
3.9	The principal components ordination of species in which the variation due to age of stand has <u>not</u> been removed.	39 40

LIST OF FIGURES (CONT'D.)

3.10	Schematic diagram showing changes from "time-out" to "time-in" ordinations.	41
3.11	The "time" species ordination.	43
3.12	Changes in species abundance in different community types.	44, 45
3.13	Changes with age of species number and canopy cover for different community types.	50

LIST OF PHOTOGRAPHS

Photo

- | | | |
|----|---|----|
| 1. | 51,000 hectare lightning fire near Selywin Lake,
Caribou Range. | 2 |
| 2. | Closed canopy white spruce and black spruce-
feather moss forest on NW facing slope, 145 years
since last fire. | 20 |
| 3. | Open canopy black spruce, white birch-lichen forest
on NE facing slope, 155 years since last fire. | 21 |
| 4. | Aerial view of open black spruce, glandular birch-
lichen woodland, 95 years since last fire. | 22 |

ACKNOWLEDGEMENTS

First we should like to thank Northwest Lands and Forest Service, particularly John Gilmour, Howard Gray and Eddy Powder for their co-operation when we were in the field and for information they provided during the analysis. Collection of data in the field was capably handled by W. Harris, S. Johnson, R. Godwin, A. Lincoln, T. Trottier, and K. Trynor. We also thank M.A. Jasieniuk and A.K. Bossort for their helpful comments during the research.

Taxonomic assistance was provided by N.A. Skoglund and V.L. Harms, University of Saskatchewan (Vascular Plants), J.H. Hudson, University of Saskatchewan (Carex and Eriophorum), D. Vitt, University of Alberta (Bryophytes).

We also thank R.L. Bailey for his help in the programs for estimating the Weibull parameters and G.A. Yarranton for editorial assistance.

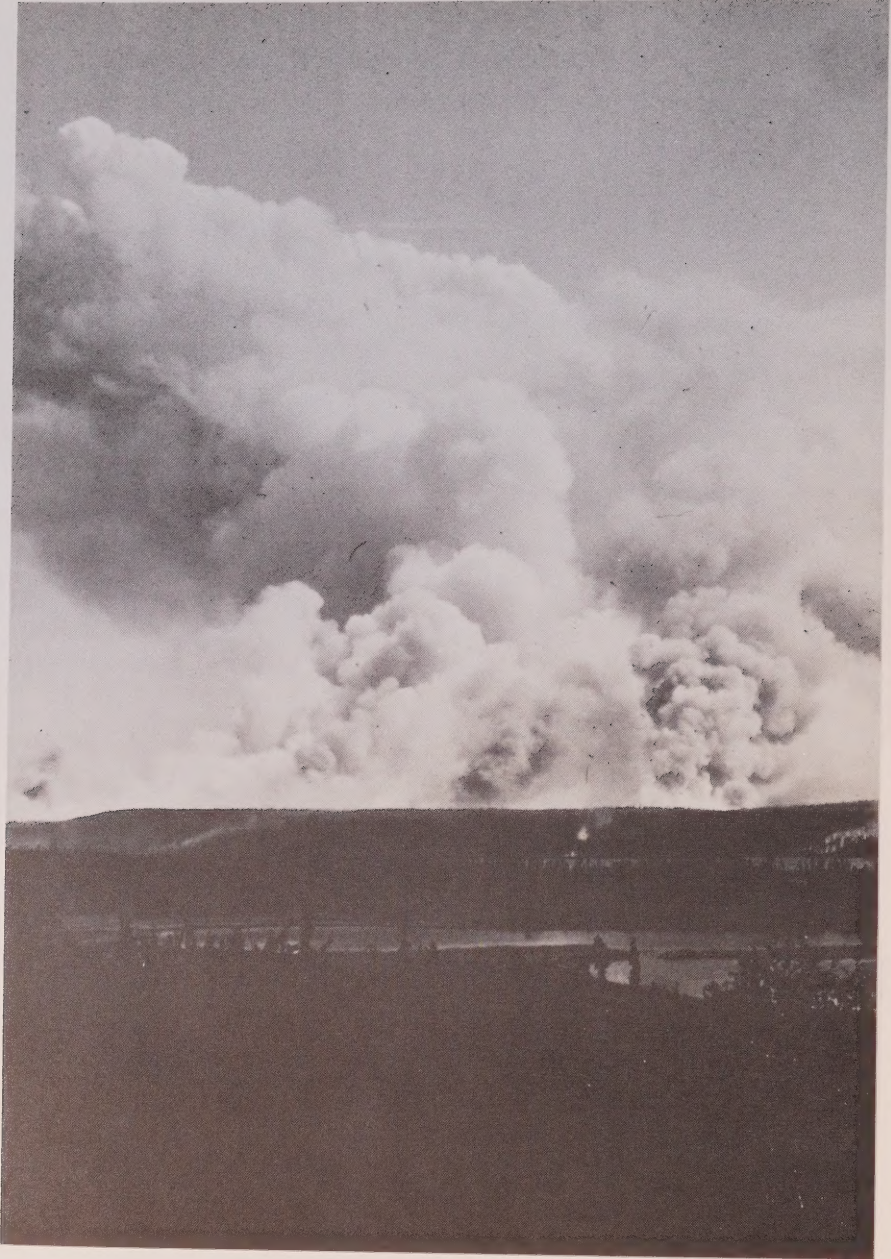


PHOTO 1

51,000 hectare lightning fire near Selywin Lake, Caribou Range.

1. INTRODUCTION

The Caribou Range (Figure 1.1) is a large (approximately 105,000 sq km) area of western subarctic forest extending from 60°N latitude north to the tree line and from longitude 104°W to 112°W. It is the wintering ground for the Beverley caribou population. It is an excellent area in which natural ecosystems can be studied with little confounding influence of man. This is particularly useful for studies of the recurrence of natural fires and resulting vegetation change.

The studies reported here are regional or geographic in scope. They are continuations of and additions to other studies in the Caribou Range (Rowe and Johnson 1975, Johnson and Rowe 1975, Rowe et al. 1975, Johnson 1975, 1976). Studies in the past and those reported here are of both basic and applied interest.

This report gives details on two objectives:

1. To develop a method for determining the fire frequency for a region; specifically, to elucidate the fire frequencies for the Caribou Range and relate this to environmental parameters and vegetation change.
2. To study changes in the composition of vegetation on uplands following fire and to describe quantitatively these changes in plant populations along temporal and environmental gradients.

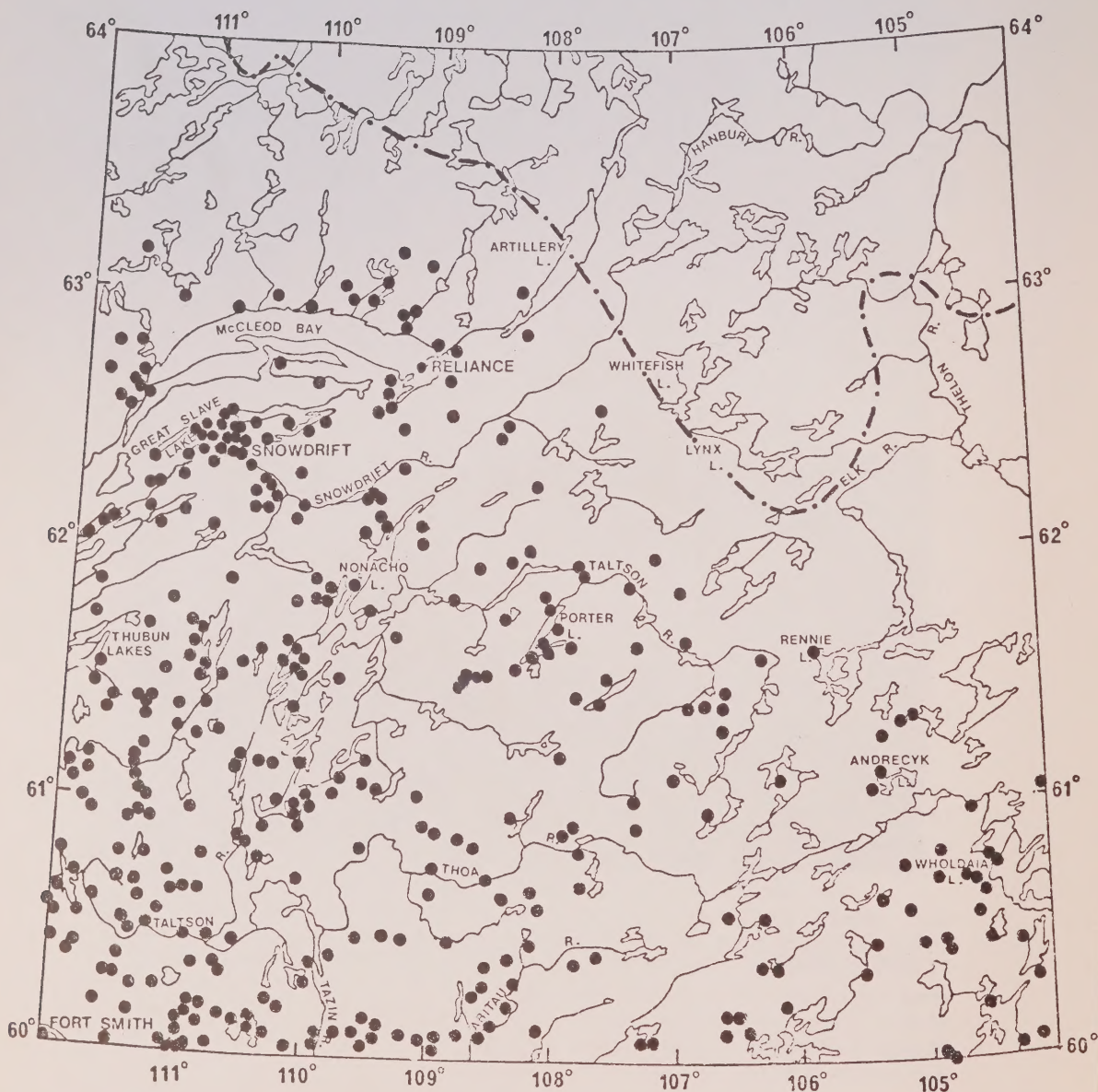
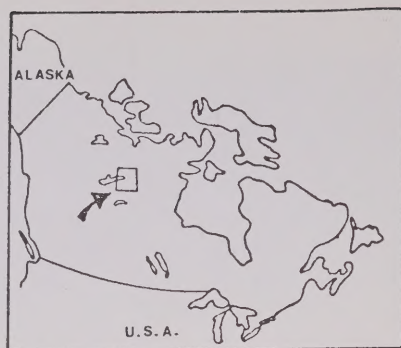
The field work was conducted by float plane and boat from base camps at Nonacho Lake, Porter Lake, Andreycyk Lake and from the settlements of Snowdrift and Fort Smith.

1.1 Physiography and Glaciation

The Caribou Range is located on the Precambrian Shield and consists mainly of an Archaean crystalline basement with Proterozoic intrusives. Rock types are mostly massive granites, gneissic granites, and granodiorites, overlain by a glacial drift veneer of varying thickness (Camsell 1916, Hoadley 1955, Taylor 1956 and 1959).

The surficial geology has not been studied systematically and, except for scattered notes in the above-mentioned reports, little information exists on the landforms and Pleistocene history. Craig (1964) and Wright (1967) reported on the surficial geology of the area north of 62° latitude and east of 105° longitude, providing useful information that can be extrapolated to the Caribou Range. Figure 1.2 gives a provisional map of the surficial geology based on air photo mosaics scaled at 1:60,000.

Figure 1.1 Map showing location of Caribou Range, N.W.T. Dots represent fires from 1966 to 1975. --- Approximate white spruce tree line.



CARIBOU RANGE - SURFICIAL GEOLOGY

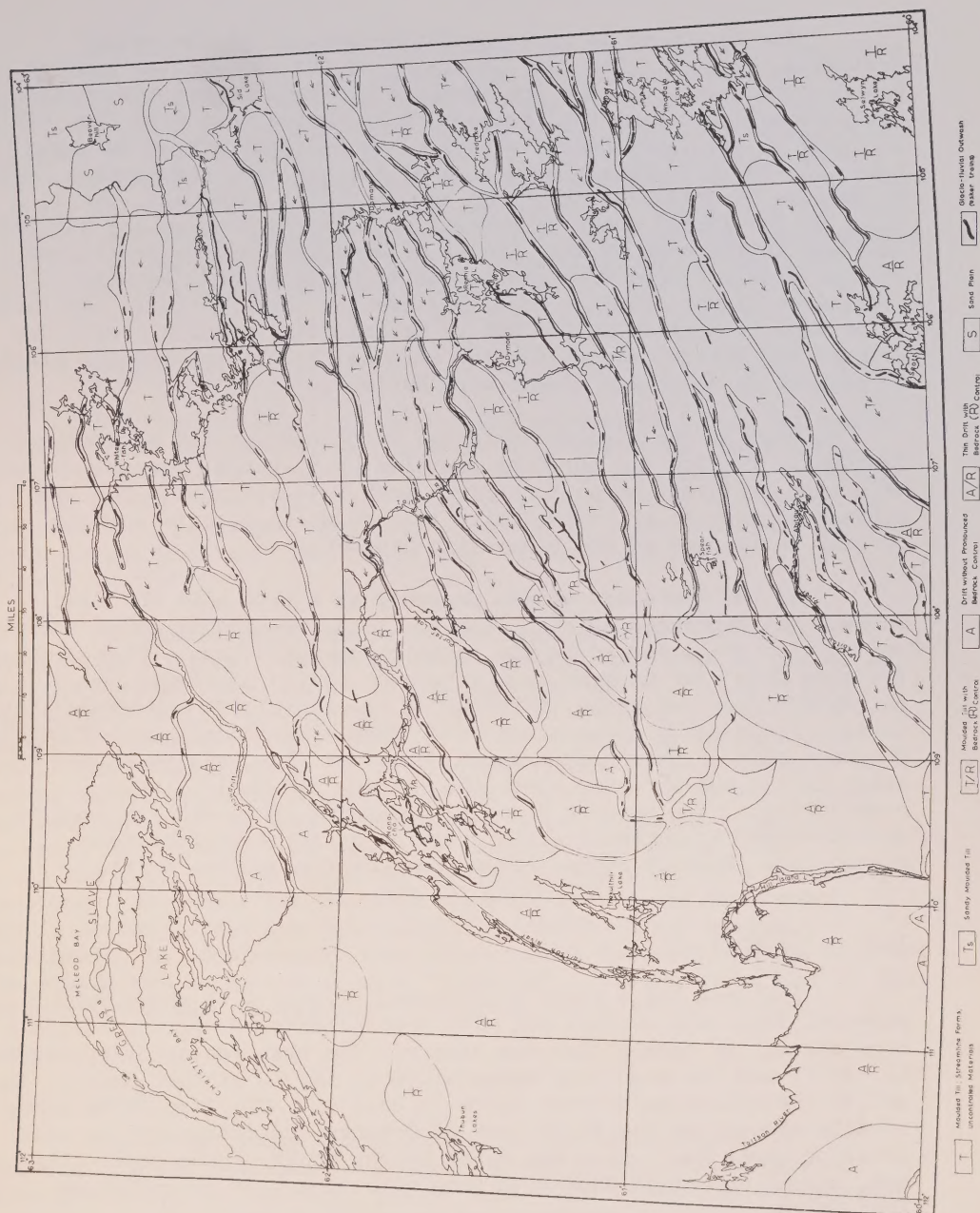


Figure 1.2 Map of landforms in the Caribou Range, N.W.T. with drumlinized drift (T) prominent east of 108° longitude and thin bedrock controlled drift prominent west of 108° longitude. Note the trains of ice-contact drift (chiefly eskers) that traverse both kinds of terrain from east to west.

The following is our speculative account of the recent geological history. The last incursion of the continental glacier was from the east, and the ice advanced westward across the north-south topographic high that extends on an approximate axis from 63° latitude at Artillery Lake (450-480 m) to 60° latitude at Dunvegan Lake (550-600 m). Possibly because of its upslope, compressive flow or because of moldable rock types and surficial materials, the thinning ice formed numerous streamlined features both on the highland axis and to the east of it. Fields of drumlins in deep drift, and bedrock drumlin forms with shallow drift (some associated with transverse ridges of minor moraines) are the characteristic landforms of perhaps two-thirds of the area. Occasionally drumlin crests are grooved and kettled suggesting the molding, by the readvancing glacier, of outwash in which ice blocks were buried.

West of the highland axis the terrain shows few streamlined features. The ice did not form drumlins or flutings, possibly because of a more resistant granitic surface rock. On air photos the land surface appears to be covered with thin ablation materials whose "grain" is imposed by the underlying bedrock.

As the ice sheet waned, probably at a time when the land surface was depressed by the prior ice load, tremendous esker trains and outwash areas formed in the local topographic lows. They cross the area from east to west in spectacular series of single and multiple ridges and knobs, interrupted by sand plains and sandy-shored lakes. These sandy areas often have large wind-eroded patches. On the west side of the Caribou Range, at about 110° longitude, the esker trains end abruptly where the Taltson and Tazin Rivers reestablish a south-north trending drainage. This western area is characterized by generally thin ablation drift, mostly bedrock controlled. Bedrock ridges often protrude through the drift.

1.2 Climate

The area has a humid continental climate with short cool summers, long cold winters and with precipitation occurring slightly more during the summer than the winter. The mean January temperature is -26°C* and the mean July temperature is 16.9°C at Fort Smith. The annual precipitation at Fort Smith is 33.1 cm. The first snow cover usually appears by the first week of October and disappears in late April or early May. Snow may occur in any month of the year. The mean annual number of days with snow more than 2.54 cm is 200 at Fort Smith.

Freeze-up of lakes occurs about the beginning of October, and break-up about the first of June. Freeze-up and break-up on the east arm of Great Slave Lake—a large body of water—are delayed several weeks (Wright 1951).

*All meteorological data courtesy of Atmospheric Environment Service, Ottawa.

Bryson (1966) studied the climate of the ecotone of the boreal forest and tundra in central Canada (see also Larsen 1965, 1971). He postulated a narrow transition zone between the cool, dry, stable Arctic air mass to the northeast and the warm, moist, unstable Pacific air mass to the southwest. This zone of climatic transition moves seasonally across the region in a northeast-southwest pulse occupying a modal July position in the region of treeline. After July the zone retreats southwest, reaching a modal winter position near the southern boundary of the boreal forest. This transition zone is usually associated with increased frontal activity.

1.3 Vegetation

The Caribou Range includes small patches of tundra and parts of two forest sections in the Halliday classification (Rowe 1972), viz. from southwest to northeast, the Northwestern Transition (B.27) and the Forest-Tundra (B.32). These vegetation belts correspond to what Hustich (1949) and Hare (1950) recognized east of Hudson Bay as "Open Boreal Woodland" or "Taiga" and "Forest-Tundra Ecotone" or "Forest Tundra".

The general physiognomy of the vegetation in the Caribou Range is as follows: Upland sites are mostly dominated by closed or open forests of black spruce (Picea mariana) and jack pine (Pinus banksiana). White spruce (Picea glauca) is a common component of forests on coarse-textured materials, for example on outwash sand plains and esker ridges. It is also the prominent tree adjacent to moving water, reaching a large size on alluvium. It is very common on areas adjacent to Great Slave Lake. Aspen (Populus tremuloides) is not a conspicuous tree except in areas of pronounced relief in the south and west. White birch (Betula papyrifera), on the other hand, is common throughout the forested area and extends to the tundra edge. Lowland sites are generally dominated by black spruce, accompanied in considerably less abundance by tamarack. As on uplands, the stands may be closed or open "peatland". Towards tree line in the forest-tundra zone, polygonally-patterned peaty ground appears.

1.4 Fire

Figure 1.1 shows the distribution of forest fires for ten years in the Caribou Range. A total of 398 forest fires occurred with 87% caused by lightning (Table 1.1). The total area burned was 1.7 million acres with large variation from year to year. These results are similar to records in the Mackenzie Valley, N.W.T. (Rowe et al. 1975), Yukon (Requa 1964, Kiil 1971) and Alaska (Barney 1971). Fire incidence seems to follow a seasonal pattern advancing from the

Table 1.1

Summary of Forest Fires in the Caribou Range 1966-1975

	<u>April</u>	<u>May</u>	<u>June</u>	<u>July</u>	<u>August</u>	<u>Sept.</u>	<u>Total</u>
Total Number Fires	1	7	114	168	106	2	398
No. Man Caused Fires	1	5	13	18	13	1	51
No. Lightning Caused Fires	0	2	101	150	93	1	347
	<u>April</u>	<u>May</u>	<u>June</u>	<u>July</u>	<u>August</u>	<u>Sept.</u>	<u>Total</u>
Total No. Acres Burned *	12	26	254,924	1,243,010	189,130	2	1,687,104
No. Acres Man Caused Fires	12	26	2,109	205	46	1	2,399
No. Acres Lightning Caused Fires	0	0	252,815	1,242,805	189,084	1	1,684,705

*Indicates only month in which fire started

south towards tree line in the summer and retreating in the fall. This leads to the recurrence of more and larger fires in the southwest and fewer and smaller in the northeast.

The seasonal patterns of lightning fires appear to be related to the conditions associated with air masses and to their movements. Lightning storms usually occur in areas under the influence of maritime Pacific air either along fronts or within isolated convective systems (Johnson and Rowe 1975). Years in which few fires occur have been shown to be related to above-normal precipitation during the summer fire season. This above-normal precipitation keeps the duff moisture at a level which generally will not support a fire.

Meteorologically the above-normal precipitation seems to result from an anomalous surface water temperature in the north Pacific. This anomaly gives rise to an amplified long (Rossby) wave which increases the convergence along the contact between the maritime Pacific and continental Arctic air masses (Johnson 1976).

2. FIRE FREQUENCIES IN THE CARIBOU RANGE

It is the objective of this section to develop a quantitative approach to fire frequency analysis, contributing to an understanding of the role of fires in the subarctic ecosystem.

Very few studies of the pattern and recurrence of fires have been undertaken. We discussed some of the recent ones in last year's ALUR report (Rowe *et al.* 1975). Of these studies, most have been essentially chronologies (e.g. Frissel 1973, Heinzelman 1973, Houston 1973, Rowe *et al.* 1974). This approach although at times interesting, is of little help in understanding the role and pattern of fire in the landscape and its relationship to the ecology of the vegetation.

2.1 Methods

A random sample of sites was taken in four regions of the Caribou Range (Table 2.1) using the following technique: Within each of the four regions, samples of approximately 10 ha were located on a map grid using random numbers. The individual samples were then located using float-equipped aircraft to reach the nearest lake and thereafter by walking. All regions sampled had been recently burned so all age intervals represent fire-to-fire events.

Dates of fires at each sample site were determined from an investigation of fire scars and tree ages. Several trees were examined at each sample site. Fire scars give fairly exact ages of fires while tree ages (total rings at the base) are less dependable indicators. The reason is that all trees do not regenerate immediately after a fire, there often being a patchy and sporadic establishment for some years after. Only maximum ages can then be expected to provide useful clues to fires. Areas where trees have survived more than one fire require careful investigation both of fire scars and of the distribution of tree ages.

For theoretical reasons, the Weibull distribution (Weibull 1951) has been selected to describe fire frequencies. It has two parameters of interest:

- (1) The scale parameter "b" characterizes the expected recurrence of fire; i.e. a small value indicates a short time in years between fires.
- (2) The shape parameter "c", as the name implies, determines the shape of the distribution of intervals between fires. A shape value of approximately 3.6 gives a normal distribution and

Table 2.1 Location and information on regions sampled in fire frequency studies.

Region	Long.	Lat.	Size Region Sampled	No. of Fire Intervals	Tree Composition	Remarks
Whirlwind Lake	108° 42'	60° 13'	5x5 km	25	Jack pine-black spruce	Area last burned 1972
Pilot Lake	110° 43'	60° 31'	10x10 km	25	Jack pine-black spruce	Area last burned 1971
Rutledge Lake	110° 30'	61° 44'	10x10 km	36	Black spruce- jack pine	Area last burned 1971
Siltaza Lake	109° 38'	62° 12'	5x5 km	15	Black spruce- jack pine	Area last burned 1971

values less than this give a more positively skewed distribution until it becomes simply monotonically decreasing (see bottom of Table 2.2 page 13).

The parameters of the Weibull were estimated by three methods: a transformation approach (Menon 1963), a linear function (D'Agostino 1971) and Maximum Likelihood (Harter and Moore 1965). The differences between these techniques were slight and so only the results by the D'Agostino linear function method are presented in Table 2.2.

Goodness of fit was tested between the expected distributions from the estimated parameters and the observed data, using the Kolmogorov-Smirnov statistic (Sokal & Rohlf 1969). In all four cases the difference between the expected and observed distributions was less than that expected by chance at $\alpha = 0.01$.

2.2 Discussion

As we have seen, the empirical evidence fits well to the Weibull distribution. The question now is: what ecological meaning can we attribute to the distribution's parameters? The argument we will present relates expected fire recurrence time (parameter b) to regional climate and the shape (parameter c) to local topography and substrate.

The expected fire recurrence (b) should change in a consistent manner between regions as the air mass climate and ignition pattern change. In the area east of Great Slave Lake the air mass climate generally changes perpendicular to tree line (Larsen 1965, 1971, Bryson 1966; Barry 1967; Mitchell 1973). This change can also be seen in the meteorological relationships of the components of the Canadian Fire Weather Index in the map of Simard (Figure 2.1). The Fire Weather Index is particularly useful because it relates meteorological parameters to fire spread and intensity (Van Wagner 1974), bridging air mass characteristics and fire behaviour. Figure 2.1 shows the decreasing frequency of high FWI values towards tree line and thus the decreasing likelihood of fire occurrence. This is known to be the case for actual fire occurrence for the last 10 years for the Caribou Range (Johnson & Rowe 1975 and unpublished). The ignition source, lightning¹, also changes perpendicular to tree line as would be expected (Kendall & Petrie 1962).

It follows that the expected fire recurrence parameter (b) should increase towards tree line, i.e. as the regional climate becomes less conducive to fire the expected time between burns should increase.

¹Lightning accounts for 99.9% of the area burned in the Caribou Range.

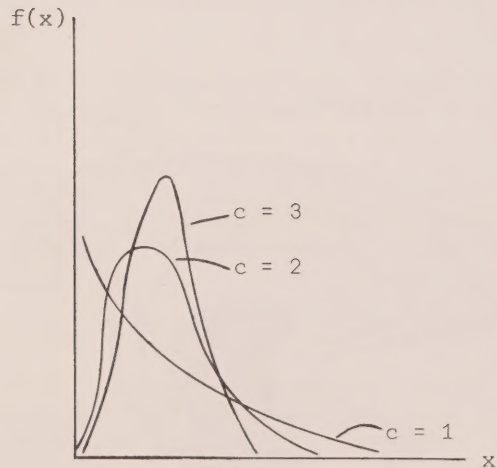
Table 2.2 Fire Frequency Weibull Parameter estimates using the method of D'Agostino (1971). b is the scale and c is the shape parameter.

	b	c
Whirlwind Lake	55.52	2.64
Pilot Lake	69.02	3.19
Rutledge Lake	96.75	2.13
Siltaza Lake	101.11	4.43

Weibull Density Function

$$f(x) = \frac{c}{b} \left(\frac{x}{b} \right)^{c-1} \exp \left[- \left(\frac{x}{b} \right)^c \right]$$

$$b > 0 \quad c > 0$$



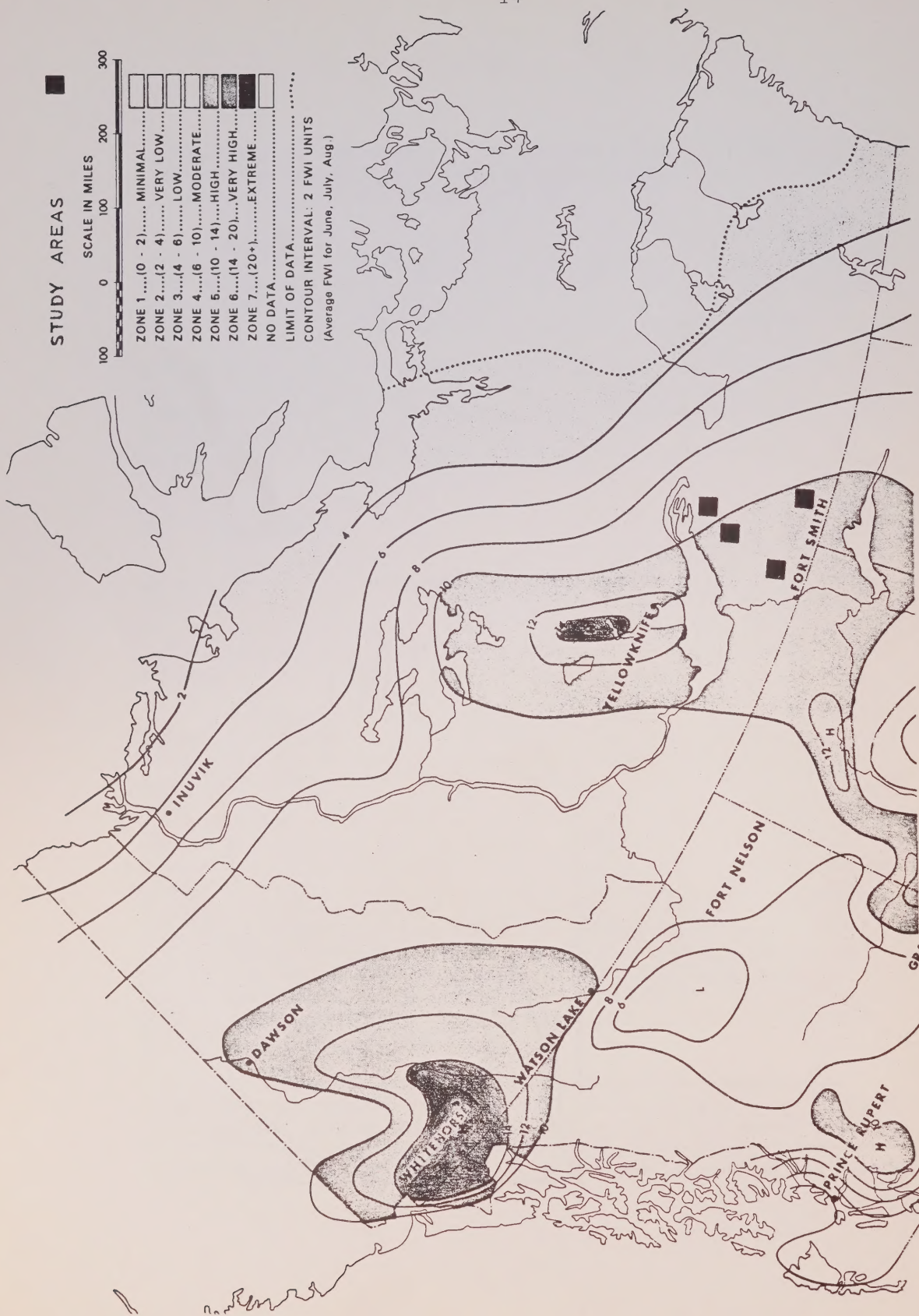


Figure 2.1 Changes in Canadian Fire Weather Index (FWI) as calculated from Meteorological parameters (from Simard 1974). Notice the decrease in FWI towards tree line.

Figure 2.2 shows this to be the case, the expected interval between fires (b) increasing as tree line is approached.

The shape parameter (c) should be related in a consistent manner to variability of the local climate and substrate. To measure local climate and substrate over large areas is nearly impossible, so an indirect approach was taken. This approach assumes that the diversity of topoclimate and substrates is related to the complexity and roughness of the terrain (Hayes 1941, Byran and Jemison 1943, Geiger 1965). Thus in any relatively small area, smooth terrain should have uniform topoclimate and substrate while rougher terrain should have a variety of topoclimate and substrates.

A method of measuring terrain roughness developed by Hobson (1967, 1972) was used. This is a vector dispersion approach; it determines a planar surface using the 3-dimensional orientation of three adjacent elevational readings. A unit vector is then constructed normal to this surface. The dispersion of all such vectors for a sample region is then calculated. High vector dispersion indicates terrain with many slopes and aspects while low vector dispersion indicates a relatively uniform terrain.

A grid was laid out on National Topographic Surveys maps at 1:250,000 over the 4 sampled regions. Elevations were determined at 2 km intervals for a total of 36 readings in each region and the vector dispersions calculated.

Figure 2.3 shows the vector dispersion values plotted against the shape parameter (c). The higher the vector dispersion the more varied the terrain and vice-versa. Therefore the rougher the terrain the more positively skewed are the intervals between fires, and the smoother the terrain the more symmetrical is the distribution of intervals between fires.

It would appear that in regions of smooth terrain the differences in fire susceptibility between sites are greatly reduced, and the age differences between sites take on a random distribution around the expected value. In varied terrain the difference in fire susceptibility between sites is larger and thus a greater variety of ages between fires is found. In this latter case there are more older fire resistant sites and the distribution is positively skewed.

2.3 Implications

It is important to stress the hierarchical nature of the two Weibull parameters. The expected recurrence time of disturbance (b) seems related to the regional climate and landforms and thus is related to the regional frequency and intensity of fire. This regional effect in turn sets the bounds in which the shape parameter (c)

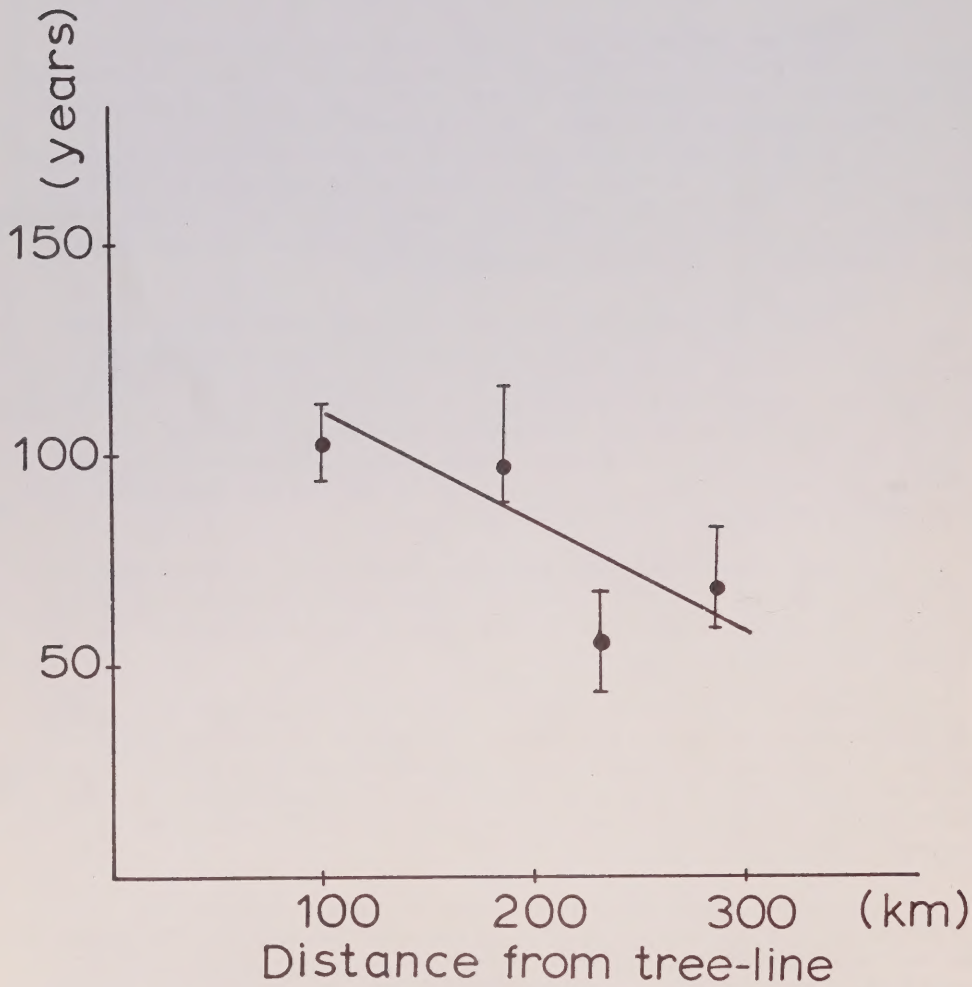


Figure 2.2 Relationship of distance from tree line (regional climate) and expected fire recurrence for regions. Tree line is defined here to be the region in which trees cease to appear on the uplands although they may still appear in the stream valley. Bars represent 90% confidence intervals for the parameter.

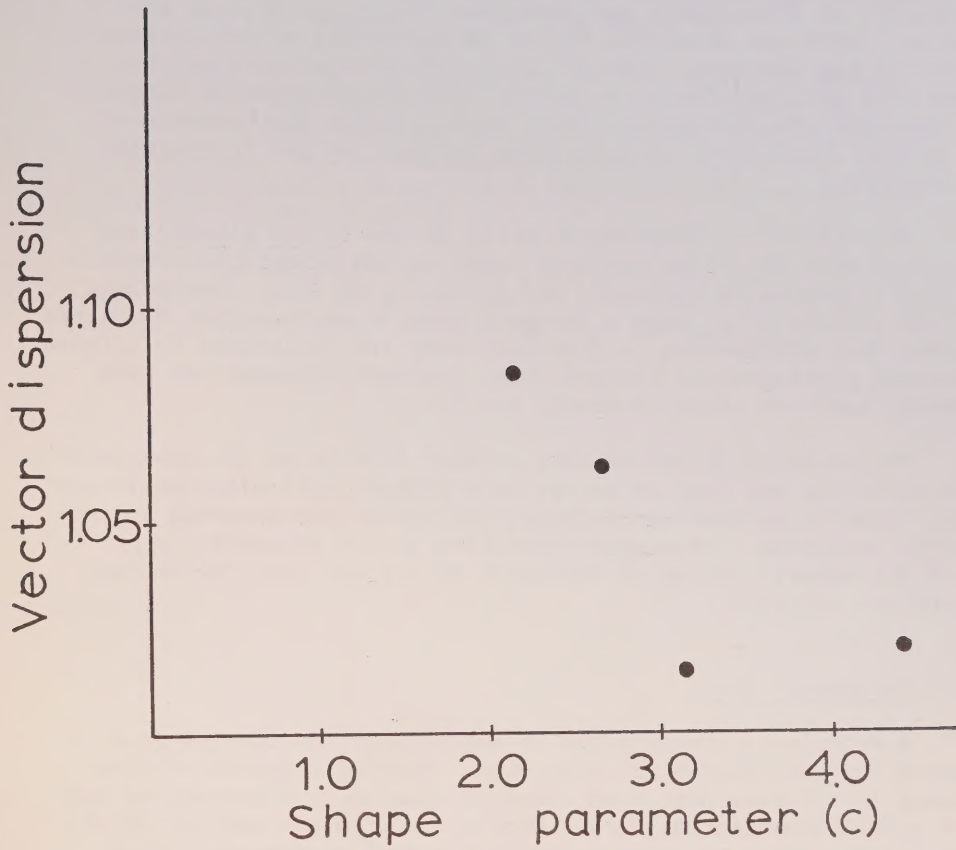


Figure 2.3 The relationship of Vector dispersion (Terrain Roughness) and Weibull shape parameter.

operates. The shape parameter reflects the modified regional situation due to the local topography such as slope, aspect, elevation and substrate, influencing the variation in fire recurrence from the expected value.

Note particularly that both frequency and intensity (fuel consumption) of disturbance are accounted for by the Weibull distribution. Both are essential for an understanding of disturbance. Vogl (1970) has discussed this in his observations of pine barrens. He says "the critical factor in determining the presence of barrens among northern pine-hardwoods forest appears to be the presence of sandy plains...and fires of the proper intensities and frequencies..." (*italics ours*).

Rowe (1970) in speaking of white spruce (Picea glauca) and fire states that the differences in landform and topographic position lead to differences in frequency and intensity of fire. Heinzelman (1973) in a study of a large wilderness area in northeastern Minnesota has shown that differences in fire frequency are influenced by climate and several physiographic factors (e.g. lowlands, streams and lake alignment, landform types, bedrock, etc.).

The evidence presented here is that fire is an integral part of the subarctic and that it recurs in a probabilistically consistent manner. Fire is neither unorderable, infrequent nor external to the subarctic ecosystem. To suggest that fire in the subarctic is not part of the natural course of things is to suggest that the weather and land are not also.

2.4 Management Uses

A relatively simple means of empirically calculating fire frequency has been needed for some time. Most discussions of fire frequency in the past have been based on opinion or observations and not on actual quantitative data. Once a resource manager has at his disposal a technique to collect and calculate fire frequencies he can utilize this information to help him make several decisions:

1. In terms of fire fighting it will help him determine how to allocate pre-suppression effort. Particularly in the N.W.T. where fire reports for a reasonable period of time are generally not available this technique supplies a way of determining the pattern of fire recurrence.
2. Land-use regulation, which in the N.W.T. is the responsibility of Canada Dept. of Indian & Northern Affairs, would be helped by a knowledge of the fire frequency in a region. For example,

one of the criteria for issuing a lease, where a choice of location in two regions exists, could be in the region of lower fire frequency. The object would be to minimize the construction of permanent structures, either fishing lodges, transmission lines, radio and microwave repeaters in regions of high fire frequency.

3. As for the management of the land, the understanding of the natural fire frequency would help the land manager understand what regime of fire the ecosystem is adapted to and thus help him draw up a more comprehensive land-use plan (Wright 1974).

The technique we have suggested here needs further validation but we hope that it or its modification can fulfill this need for a means of empirically calculating fire frequencies.



Photo 2. Closed canopy white spruce and black spruce - feather moss forest on N.W. facing slope, 145 years since last fire.



Photo 3. Open canopy black spruce, white birch - lichen forest on N.E. facing slope, 155 years since last fire.



Photo 4. Aerial view of open black spruce, glandular birch - lichen woodland, 95 years since last fire.

3. VEGETATION COMPOSITIONAL CHANGE

This section examines the temporal and environmental changes in upland vegetation composition with particular reference to recovery after fire.

Note the phrase "vegetation compositional change" used in preference to "succession" because we have found, as others have (Whittaker 1957, Raup 1964, Dix & Swan 1971, Drury & Nisbet 1973, Heinselman 1973, Henry & Swan 1974, Wright 1974), that the traditional idea of succession¹ is a difficult concept to apply. Drury & Nisbet (1973) have given a good review of some of the problems.

3.1 Present State of Knowledge

Little work, even of a descriptive nature, has been done on the vegetation in the western subarctic. Maini (1966) studied a single site near tree line at the eastern side of the Caribou Range. The esker-formed island is dotted with white spruce and there are large open areas of loose sand and gravelly knolls. The lower slopes and protected valleys are covered with black spruce and lichen vegetation as are those of the surrounding till-covered mainland.

Peripheral to the Caribou Range, Larsen (1971) described several communities in the Fort Reliance-Artillery Lake area, Kelsall et al. (1971) reported on a broader natural history survey of the same locality and Argus (1966) briefly described plant communities just south of 60° latitude in Saskatchewan.

Studies of succession in the subarctic are also few. Ritchie (1958, 1959) working in the subarctic of Manitoba has perhaps had the greatest influence on the thinking of subsequent work on succession. His influence is best shown in Figure 3.1 (top) which gives a successional sequence on mesic upland sites. The mature (climax) forest is seen as a closed black spruce forest with a ground cover of feather moss (Pleurozium schreberi, Hylocomium splendens, Ptilium crista-castrensis and Dicranum spp.). Seral stages run from young birch-willow immediately after fire to jack pine to jack pine-black spruce to black spruce-birch and then the mature forest. He also recognizes edaphic climaxes of jack pine on sand and bedrock.

¹Succession is an orderly unidirectional change in plant communities, in which one set of dominants replace another as they make the environment unsuited for themselves. The terminal or climax stage is reached when a set of dominants is able to replace itself in perpetuity.

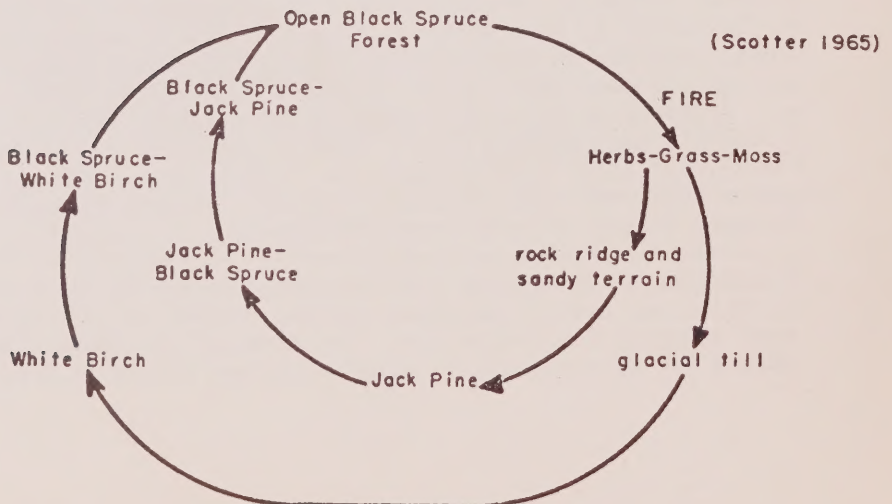
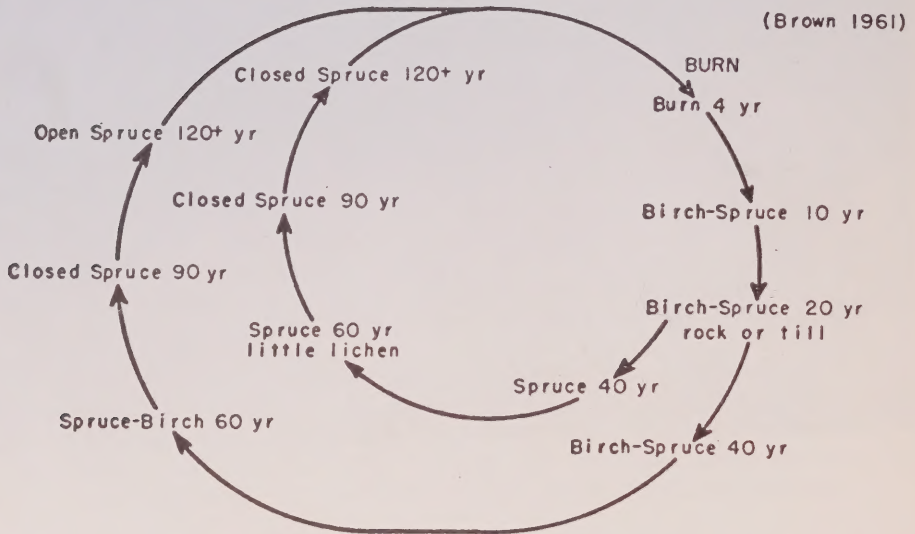
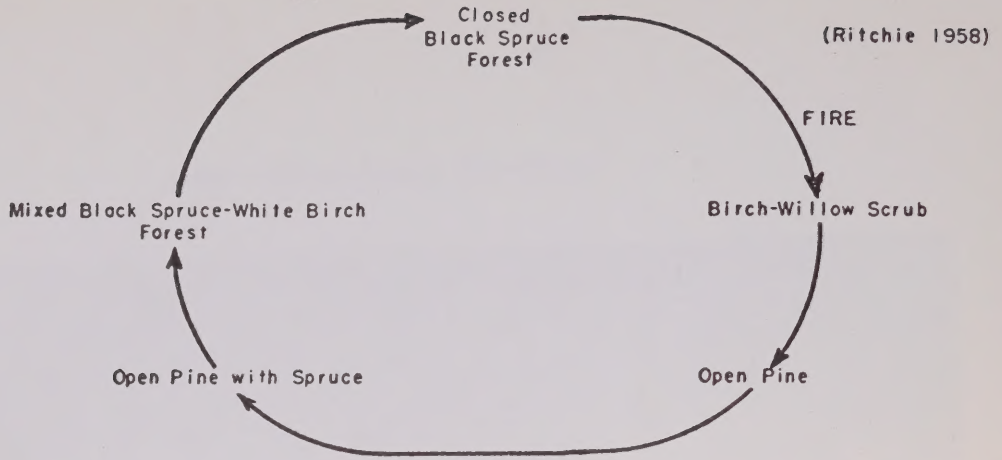


Figure 3.1 Successional sequences as proposed by the respective authors.

Scotter (1964, 1965, 1968) working in the Stony Rapids area of Saskatchewan and Taltson River area of the Caribou Range, studied the condition of the winter range of the barren-ground caribou. His view of succession (Figure 3.1 bottom) is modified from Ritchie (1958) and from aerial photo interpretation of his Stony Rapids study area by Brown (1961). The successional sequence is essentially the replacement of the less shade tolerant jack pine or birch by the more shade tolerant black spruce. Scotter is uncertain whether black spruce-lichen should be considered climax although it is capable of self-perpetuation and has a high degree of stability. However he feels that white spruce may be the ultimate climax if fire protection were given for a long enough period of time. A list of plants is given which is related to each of the stages of succession.

Kerhsaw et al. (1975) working in the Carleton Lake area of the south central Caribou Range on drumlins, has identified three stages of succession after fire. The first stage lasts about 25 years, during which Polytrichum piliferum becomes established. The second stage lasts about 60 years and sees the invasion of the lichens Cladonia alpestris, C. uncialis and Cetraria nivalis. Black spruce, the major tree on drumlins, becomes re-established during this stage. The third phase is dominated by a ground cover of Stereocaulon paschale. He suggests that a later or final stage may possibly be closed black spruce-feather moss forest.

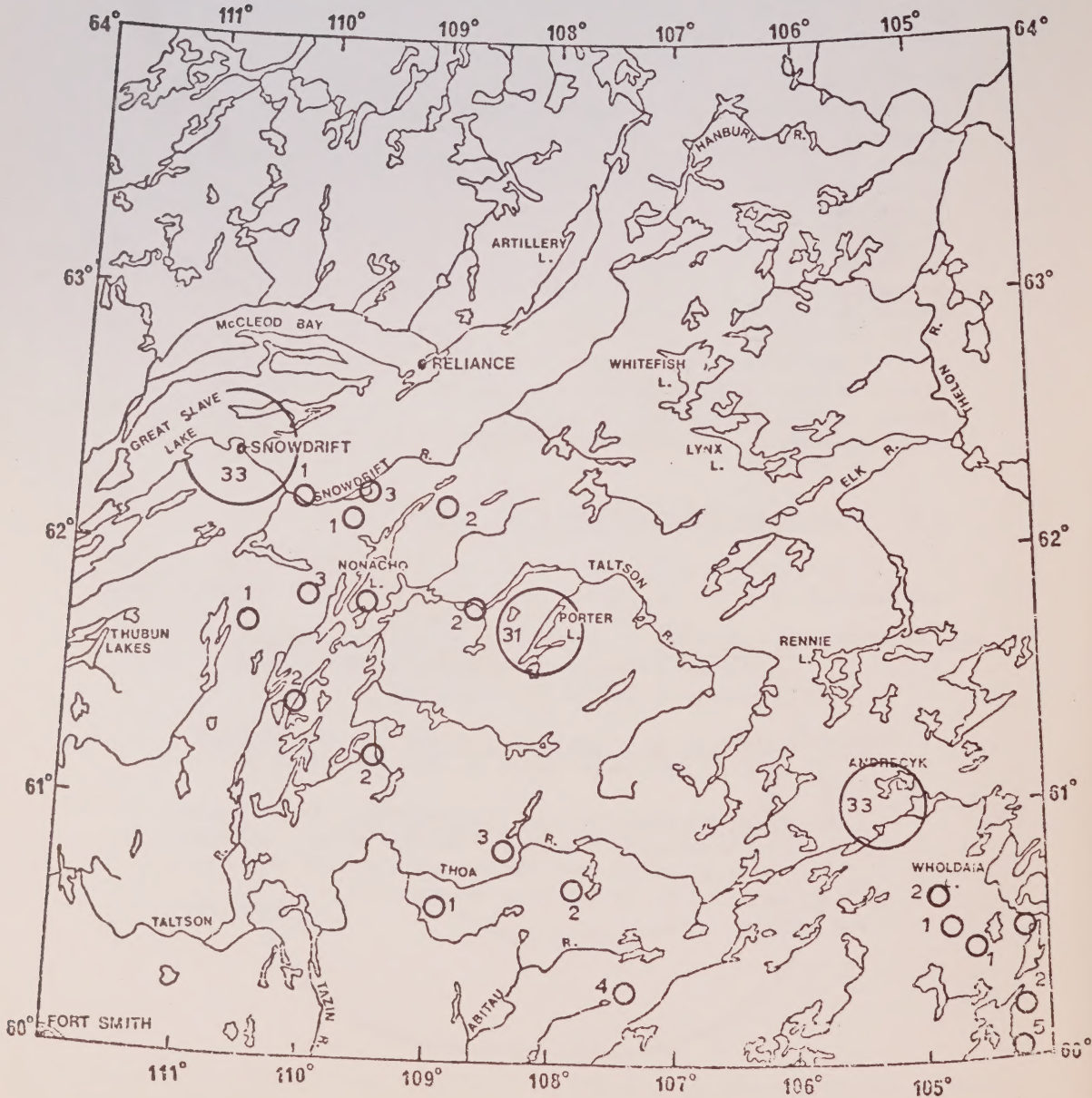
The only other successional study of interest is by Raup (1930) on the sand plains adjacent to Great Slave Lake near Fort Reliance. He describes the physiographic succession from newly emerged sandy beaches to spruce-lichen woodland on old beach terraces.

3.2 Field and Laboratory Methods

One hundred and forty-one stands of vegetation were located and sampled as shown in Figure 3.2. Stand selection criteria were:

1. Upland Sites: Vegetation rooted in mineral soil and/or no evidence of standing water or water permanently in the rooting zone.
2. Landforms and Vegetation Types: No restriction; as many different types as time permitted.
3. Size and Compositional Homogeneity: Area sampled had to be approximately four (4) ha as a minimum; the vegetation composition and physical environment had to be visually homogeneous.

Figure 3.2 Map showing the general location of the 141 stands sampled.



4. Disturbance: Areas burned by forest fires of all ages were sampled. Figure 3.3 shows the frequency distribution of stand ages. Areas disturbed by man (e.g. camp and cabin sites, tree cutting, etc.) were not sampled. Stands had to be reasonably uniform in age (see below).

Most stands were located by boat from four base camps, some as far as 25 km from the base camp. Other stands were scattered throughout the region and were reached by float-plane.

In each stand the following three categories of information were collected: (1) vegetation composition and structure, (2) physical environment and (3) age and fire history.

The vegetation was divided into "trees" (> 2 cm diameter at breast height, DBH) and "herbs-shrubs-lichens" (< 2 cm DBH). Trees were sampled using the wandering quarter method (Catana 1963, Batcheler 1971). This point sampling technique is fast and allows the determination of tree clumping as well as the usual quantitative information on frequency, density, basal area and height. The determination of clumping is particularly important in the subarctic where vegetative reproduction is an important means of propagation for two of the commonest trees, black spruce and white birch. Ten to fifteen points (40-60 trees) were sampled in each stand. Herbs-shrubs-lichens were sampled for frequency in 10 to 20 0.25 meter square quadrats, located regularly along a transect in each stand. A larger number of quadrats were used in the younger stands where the abundance of plants was low and where more quadrats were needed to reduce the error of the frequency estimation.

Stand age and fire history were carefully documented. For stands less than 10 years old, exact dates of fires were obtained from Northwest Lands and Forest Service fire records. For older stands the time since fires was determined by dating several of the largest trees plus the fire scars found on trees in the stand. An examination of these dates, and of the stand's structure in the field, allowed an estimate of the fire history. The error associated with this method of dating is compatible with the rate of compositional change. Young stands in which compositional change rate is high can be dated with very great accuracy while old stands in which compositional change rate is low (and therefore adequately related to an age range rather than an exact age) can be dated generally with less accuracy. In all the stands sampled some sign of fire was always found. It would appear that very few upland stands escape fire for longer than 300 years.

General environmental measures were made on elevation, macro-relief classes, origin and mineralogy of parent material. The moisture regime was evaluated by taking into consideration slope steepness, position on slope, water retention capacity, depth to

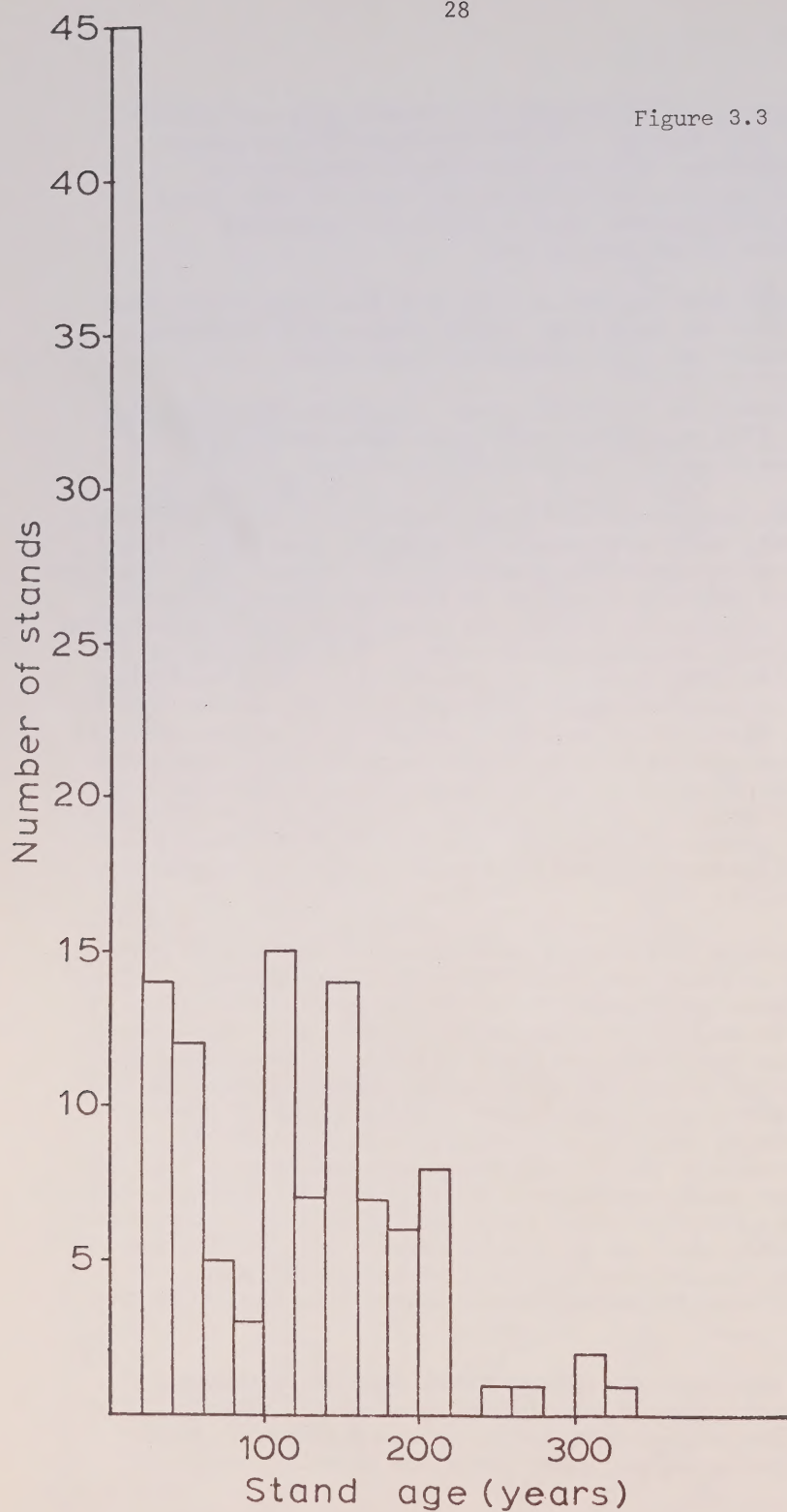


Figure 3.3 The distribution of stand ages in this study. Note: stands were not collected in a random manner, thus the distribution cannot be used to calculate the probability of occurrence of a stand of a particular age.

mottling, gleying and bedrock, stoniness, amount of bedrock exposed, depth to permafrost (if present) and soil texture. The nutrient regime was evaluated in the field according to texture, humus type and soil profile characteristics; supplementary laboratory analyses were made of pH, conductivity, % organic content, nitrate, available potassium, phosphate, calcium and magnesium.

The local climate or energy regime was evaluated using the slope, aspect and geographic location to calculate the potential direct short wave radiation (cf Furnival et al. 1969, Buffo et al. 1972). Albedo was measured with a solarimeter. The relative elevation and topographic position were used to determine night temperature relations. Other measures such as soil texture and moisture, canopy cover, and measurements of air and soil temperatures, aerial infra-red thermometer readings of selected stands were also used. The micrometeorological work by Rouse (in Kershaw et al. 1975) at Carleton Lake has proved very useful. Canopy cover was estimated visually over each quadrat.

3.3 Methods of Analysis

In the multivariate analysis of vegetation data, one of two goals is usually set. The first is to elucidate the effects of environment; in this case stands are chosen which show as little evidence of disturbance as possible. By sampling stands of stable composition, differences due to environment (the spatial gradients) are explained. The other is to elucidate the effects of time, by minimizing environmental differences and choosing stands whose differences are attributable to age. Investigators have not always kept the two aims separate, so that environmental gradients have been misinterpreted as time gradients (successional series) and vice-versa.

Analysis is likely to be both more efficient and more informative if environmental and temporal variation in the vegetation are examined separately. As a first step variation attributable to time was removed from the data by means of a multivariate linear model in which the original (raw) data matrix was regressed on a vector of stand ages. The difference between the original data and the predicted data due to the regression is a residual matrix of species correlations in which the variation due to stand age has been removed. This correlation matrix was then subjected to principal components analysis.

The 31 species used in the study are those occurring in 25% or more of the stands. In the original data the herbs, shrubs, and lichens are represented by frequencies and trees by values of a synthetic index of frequency, density and basal area. This synthetic index is a linear combination of these three variables subject to the constraints that the variance of the index be a maximum and that the sum of squares correlation between the index and the variables also be a maximum.

3.4 Interpretation of Gradients in Ordination With Time Variation Removed

Figures 3.4 and 3.5 show the species and stand ordinations using data from which the variation due to stand age has been removed. They can be interpreted in terms of two environmental gradients, heat regime and nutrient regime, without the confounding effects of differences in stand age.

3.4.1 Heat Regime Gradient

The heat regime gradient accounts for 20% of the variation in the "time free" ordination. This gradient accounts for more variation than any other single gradient. The gradient runs from warm, usually horizontal, dry, open canopy black spruce and jack pine-lichen (Stereocaulon paschale, Cladonia spp. and Cetraria spp.) to cool, basal slope, mesic, closed canopy black and white spruce-feather moss to very young burned stands. Table 3.1 gives a summary of the suggested heat regime along this gradient. The individual components of the regime will now be discussed in more detail.

The potential direct short wave radiation was calculated for a given latitude, slope and aspect (Geiger 1965, Buffo *et al.* 1972). Figure 3.6 shows the decrease from right to left of the potential direct short wave radiation. Open canopy black spruce-lichen and jack pine-lichen on the right end of the gradient tend to be found on horizontal surfaces while black spruce-white birch-lichen and black and white spruce-feather moss are found on bottom and northerly slopes. Divisions 8, 9 and 10 contain mostly burned sites which are variable in their radiation input.

The amount of direct short wave radiation which actually reaches the ground depends on the cloudiness, albedo (reflectance) and canopy cover. Assuming that cloudiness affects all sites more or less equally and that there is no daily pattern of cloudiness, only albedo and canopy primarily affect incoming short wave radiation.

Albedo as measured with a solarimeter differs between burned and different kinds of vegetated surfaces (Geiger 1965). Recent burns appear from the air to be nearly perfect black bodies, so much so that it is sometimes difficult to pick out details on the ground. However, with the growth of vegetation the albedo increases, with closed canopy black and white spruce having the lowest albedo (approx. 10-13%) and open black spruce-lichen higher (approx. 15-20%).

The % canopy cover increases along the gradient from right to left (Figure 3.6) and consequently the amount of direct short wave radiation reaching the ground must also decrease in a similar

Figure 3.4 The principal components ordination of species in which the variation due to age of stand has been removed. Numbers correspond to species listed below.

1. Picea glauca (Moench) Voss.
2. Betula papyrifera Marsh.
3. Pinus banksiana Lamb.
4. Picea mariana (Mill.) Britt. Sterns & Pogg.
5. Cladonia amaurocraea (Forke) Schaer.
6. Cladonia arbuscula (Wallr.) Rabh.
7. Cladonia coccifera (L.) Wield.
8. Cladonia cornuta (L.) Hoffm.
9. Cladonia gracilis (L.) Willd.
10. Cladonia mitis Sondst.
11. Cladonia rangiferina (L.) Wigg.
12. Stereocaulon paschale (L.) Hoffm.
13. Cetraria islandica (L.) Ach.
14. Cetraria nivalis (L.) Ach.
15. Peltigera malacea (Ach.) Funck.
16. Ceratodon purpureus (Hedw.) Brid.
17. Dicranum fuscescens Turn.
18. Dicranum polysetum Sw.
19. Hylocomium splendens (Hedw.) BSG
20. Pleurozium schreberi (Bridg.) Mitt.
21. Polytrichum juniperinum Hedw.
22. Polytrichum piliferum Hedw.
23. Ptilidium ciliare (L.) Hampe.
24. Picea mariana (Mill.) Britt., Sterns & Pogg. (seedlings)
25. Geocaulon lividum (Richards) Fern.
26. Empetrum nigrum L.
27. Epilobium angustifolium L.
28. Arctostaphylos uva-ursi (L.) Spreng.
29. Ledum groenlandicum Oeder.
30. Vaccinium uliginosum L.
31. Vaccinium vitis-idaea L.



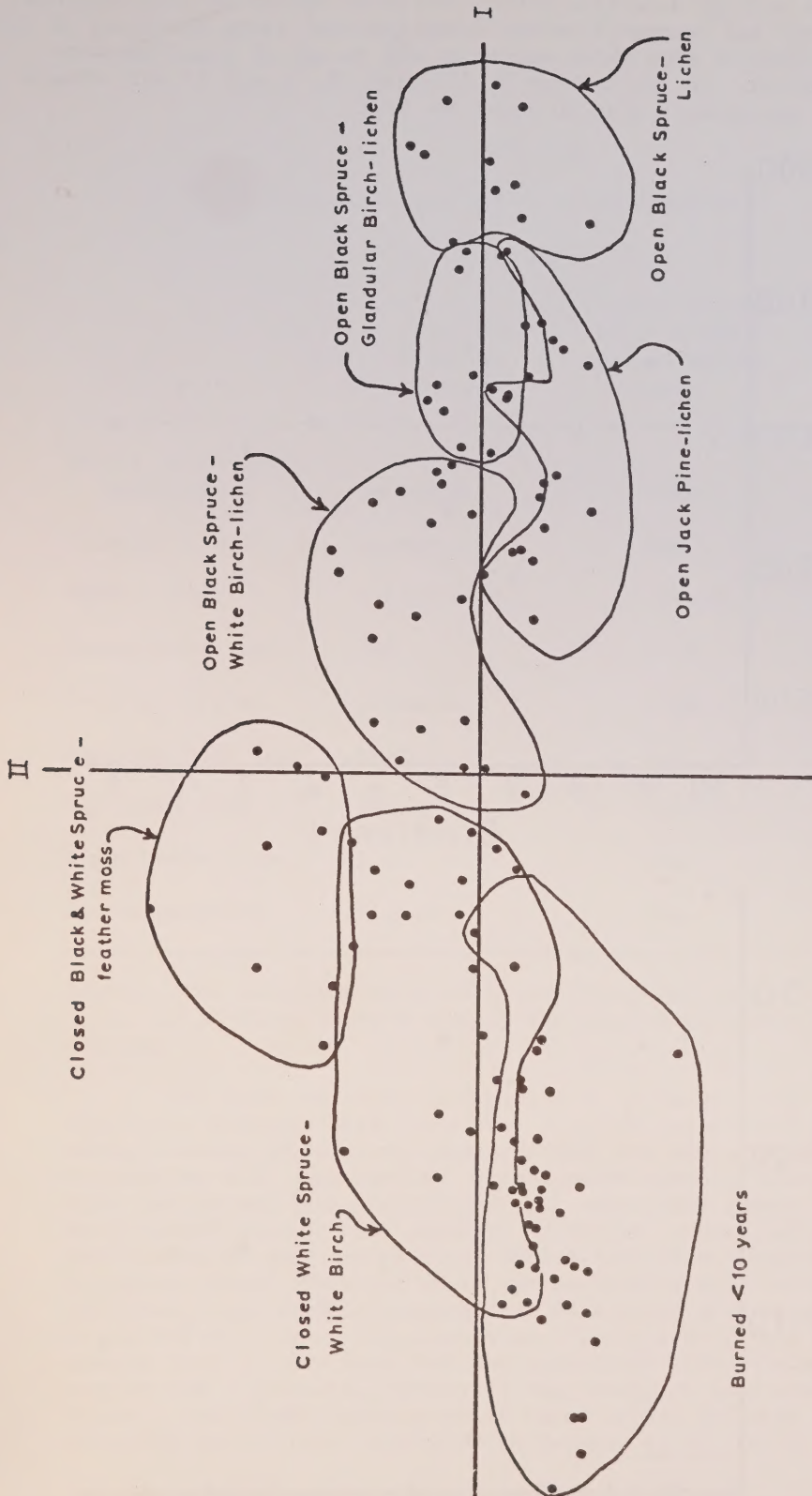


Figure 3.5 Principal components ordination of stands in which the variation due to age of stand has been removed. General boundaries of different types of communities.

Figure 3.6 The average potential direct shortwave radiation (June equinox) (top) and average % canopy cover (bottom) along divisions of the ordination from which variation due to age of stand has been removed. In the % cover in divisions 8, 9, and 10 only stands of age greater than 10 years are used.

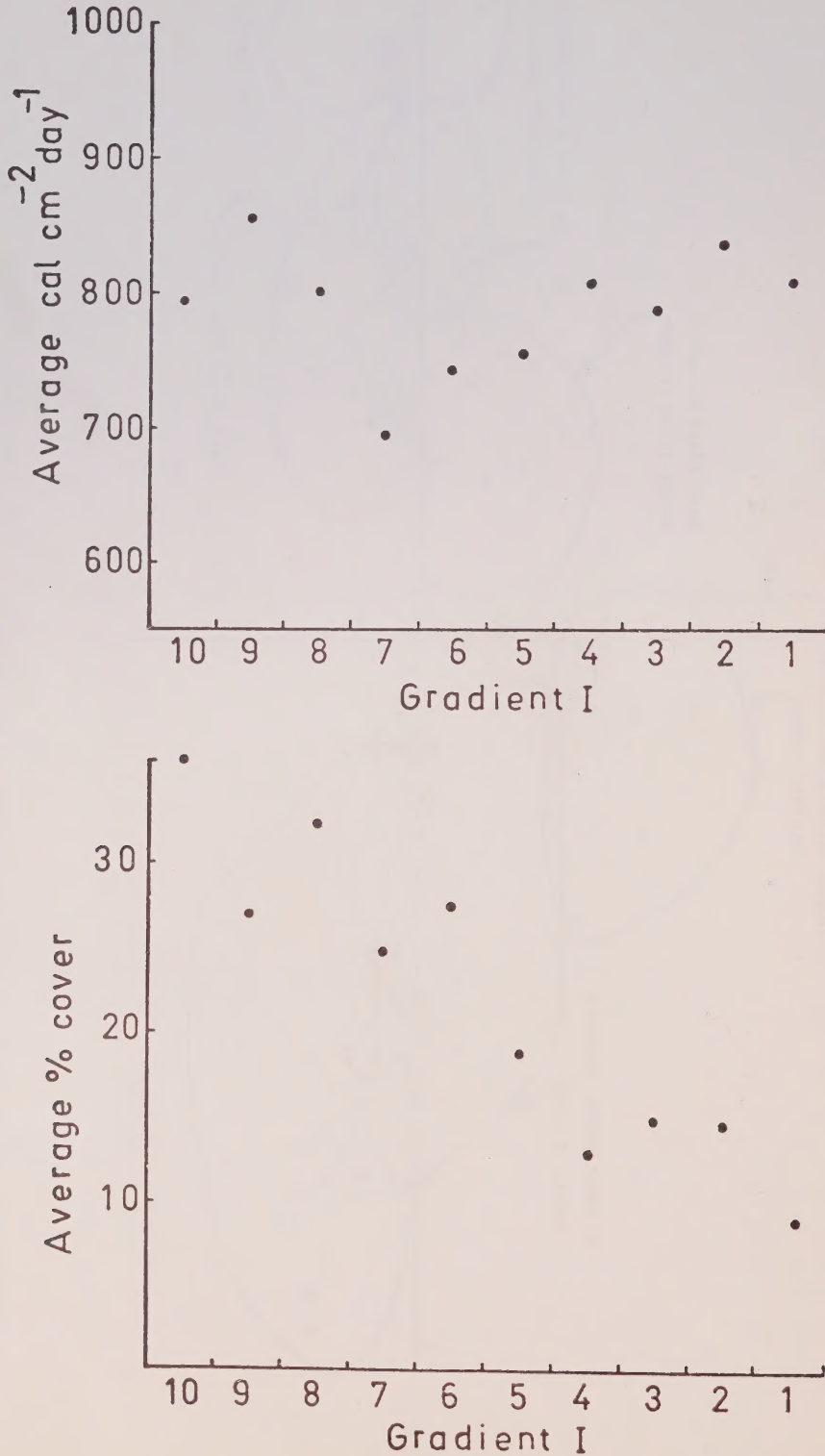


Table 3.1

Suggested Heat Regime Along Gradient I

Gradient I

	Recently burned	Closed canopy black & white spruce-feather moss	Open canopy black spruce- jack pine- lichen
Direct short wave radiation	variable	lower	higher
Albedo	lowest	low	higher
Canopy cover	little or none	closed	open
Latent heat loss	low	high	low
Moisture regime	variable	high	low
Sensible heat loss	high	low	high
Soil heat flux	variable	lower	higher
Night temperature	low	low	high
Day temperature	highest	low	higher

fashion, the exception being of course the young burns in Divisions 8, 9, and 10 which were not used in the construction of the cover average.

The input of short wave radiation is balanced by long wave radiation, sensible heat, soil heat flux and latent heat losses. Midday surface temperatures measured from the air with an infra-red thermometer rank communities: recent burns warmest, open canopy black spruce and jack pine-lichen next and closed canopy black and white spruce-feather moss coolest. Midnight screen height temperatures are warmest in open canopy black spruce-jack pine-lichen and coolest in closed canopy black and white spruce-feather moss and recent burns. The lower night surface temperatures in feather moss stands seem to be due to their lower slope position (Figure 3.7). This allows greater cool air drainage into the base slope sites (Geiger 1965) despite the compensating effect of the canopy on long wave radiation losses. Cool night temperature in burns is due to large long wave radiation losses (see also Rouse in Kershaw et al. 1975).

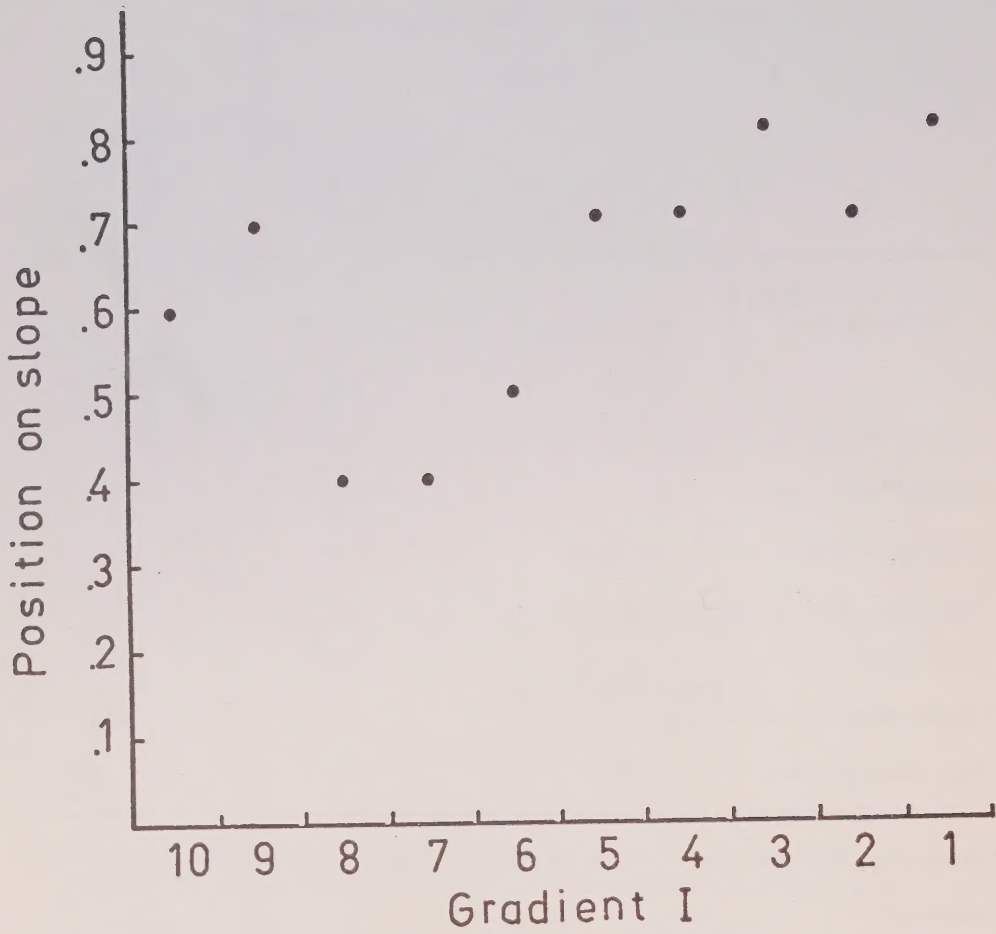


Figure 3.7 The average slope position on gradient I of the ordination in which variation due to age of stand has been removed.

Latent heat loss differs along the gradient due mainly to changes in the amount of transpirational surface (% canopy Figure 3.6) and water availability. The left end of the gradient, with the exception of the recent burns, is generally wetter. The soils in this segment of the gradient are generally mottled, finer in texture and occur in basal slope positions.

We did not measure soil heat flux along our gradient but we suggest the relationship given in Table 3.1 based on arguments given by Rouse and Kershaw (1971).

3.4.2 Nutrient Regime Gradient

The second gradient is primarily a nutrient gradient. It accounts for 10% of the variation in the "time-free" data. The gradient runs from a high nutrient, mesic end dominated by black and white spruce and feather mosses (Pleurozium schreberi, Hylocomium splendens and Dicranum spp.) to a low nutrient, dry end dominated by jack pine, lichens (Stereocaulon paschale, etc.) and some mosses (Polytrichum spp. and Ceratodon purpureus).

Figure 3.8 shows the relationship of average percent organic matter, pH, conductivity, phosphate and nitrate for 23 samples spread along gradient II. The feather moss communities are located in Division 1 and 2 and show the much higher nutrient budget with high organic content in the surface 10 cm, higher nitrate, phosphate, and calcium (not shown), conductivity and higher pH. Evidently their generally basal slope position and higher water movement leads to a continual renewal of nutrients. Therefore it is not surprising to find that these communities have greater productivity, more species and a closed canopy.

At the other end of the gradient the soil is not as loamy but more sandy. The stands consequently have low pH and conductivity and relatively low nutrients. These communities are dominated by jack pine and the slightly more fertile sites by black spruce and jack pine but both are always found with a ground cover of lichens.

3.5 Change ("time") ordination

By comparing the results of the "time-out" ordination with the conventional "time-in" ordination (Figure 3.9) of the raw data, a number of shifts occur as indicated in Figure 3.10. In Figure 3.9 the young stands are all grouped on the left side of the first axis and all others on the right; thus the energy regime gradient is replaced by a separation between very young and older stands. The nutrient regime remains more or less unaffected.

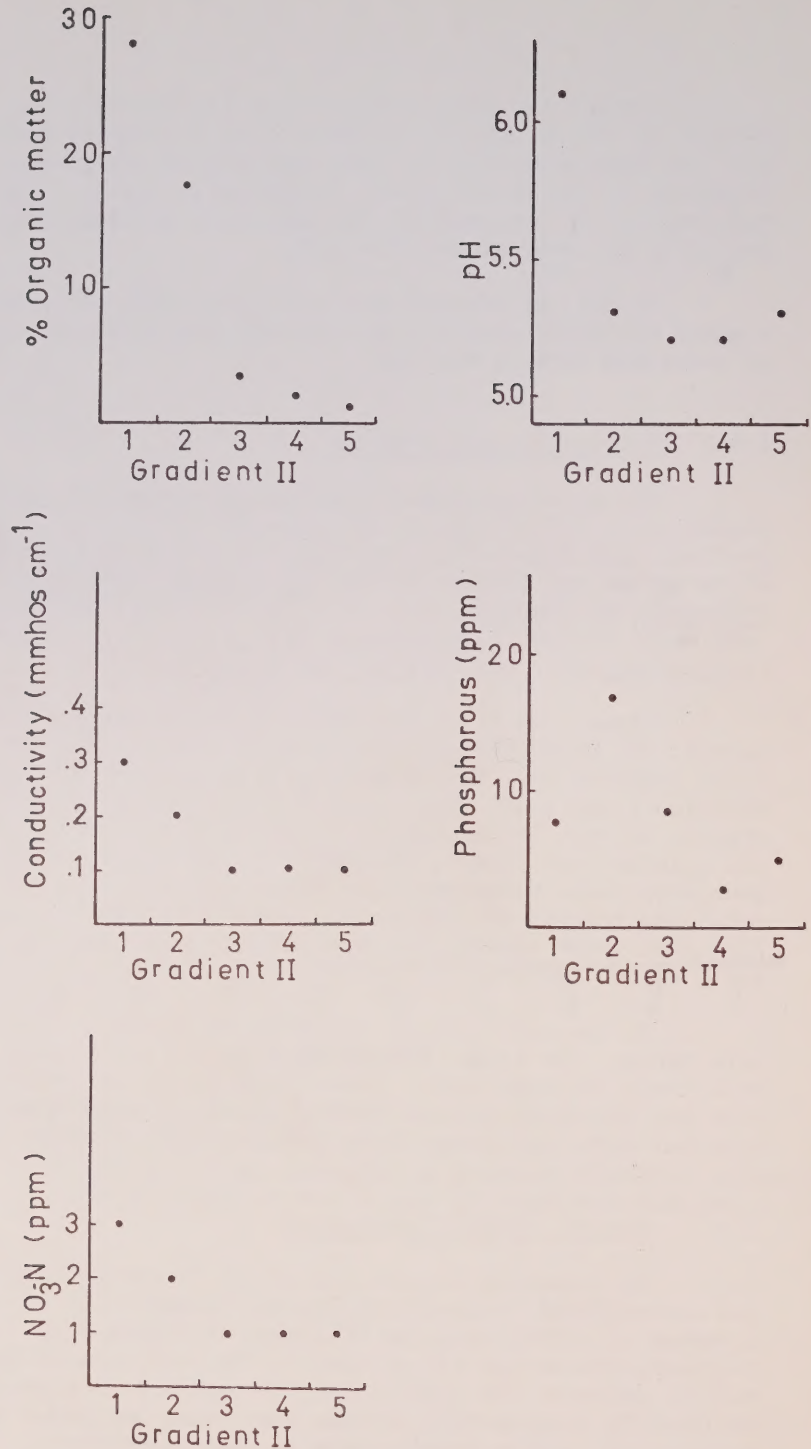
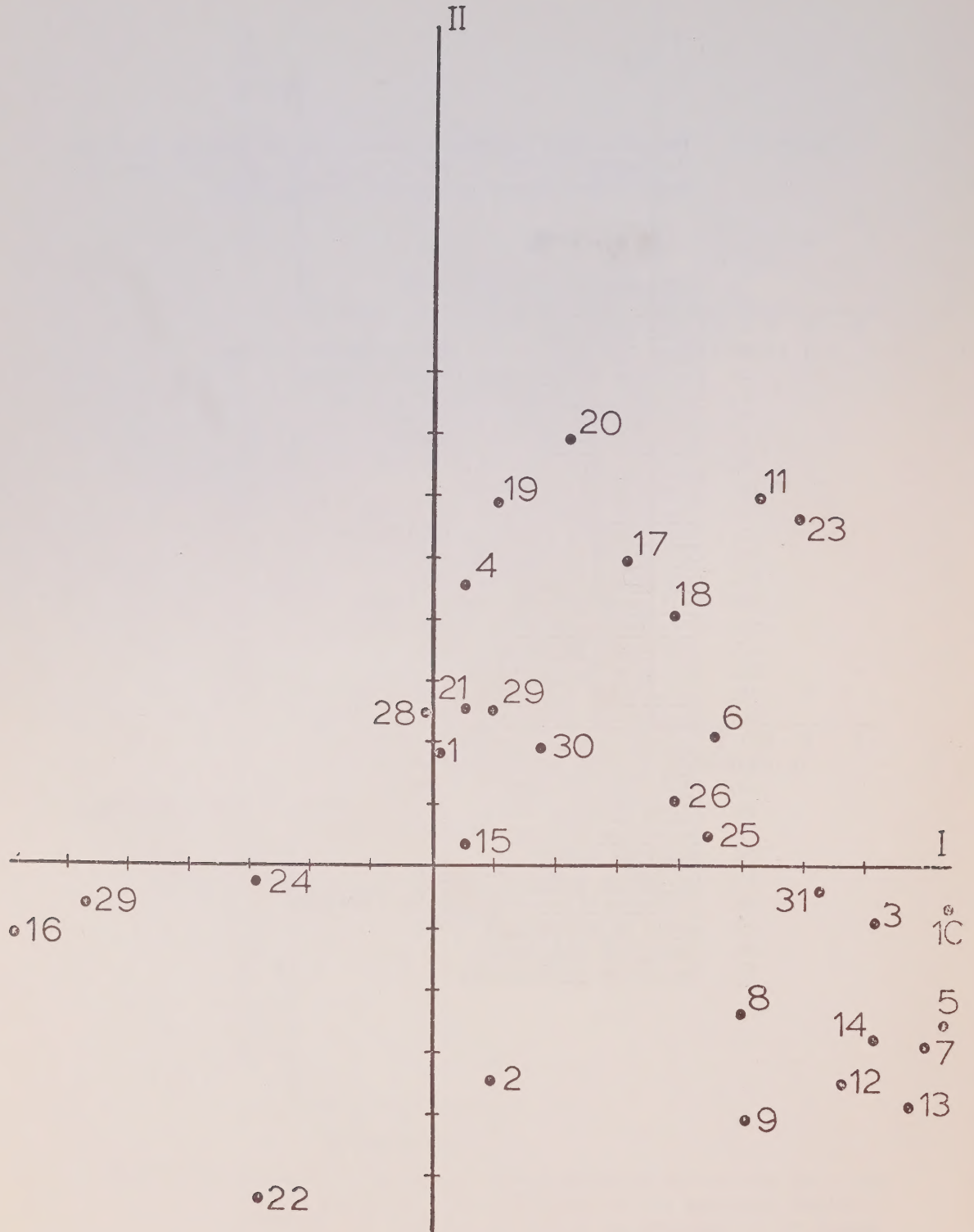


Figure 3.8 Changes in substrate characteristics across the nutrient regime gradient. The divisions on the nutrient regime gradient run from top to bottom on gradient II in Figure 3.5, i.e. divisions 1 and 2 include the closed spruce-feather moss forests.

Figure 3.9 The principal components ordination of species in which the variation due to age of stand has not been removed. Numbers correspond to species listed below.

1. Picea glauca (Moench) Voss.
2. Betula papyrifera Marsh.
3. Pinus banksiana Lamb.
4. Picea mariana (Mill.) Britt. Sterns & Pogg.
5. Cladonia amaurocraea (Forke) Schaer.
6. Cladonia arbuscula (Wallr.) Rabh.
7. Cladonia coccifera (L.) Wield.
8. Cladonia cornuta (L.) Hoffm.
9. Cladonia gracilis (L.) Willd.
10. Cladonia mitis Sondst.
11. Cladonia rangiferina (L.) Wigg.
12. Stereocaulon paschale (L.) Hoffm.
13. Cetraria islandica (L.) Ach.
14. Cetraria nivalis (L.) Ach.
15. Peltigera malacea (Ach.) Funck.
16. Ceratodon purpureus (Hedw.) Brid.
17. Dicranum fuscescens Turn.
18. Dicranum polysetum Sw.
19. Hylocomium splendens (Hedw.) BSG
20. Pleurozium schreberi (Bridg.) Mitt.
21. Polytrichum juniperinum Hedw.
22. Polytrichum piliferum Hedw.
23. Ptilidium ciliare (L.) Hampe.
24. Picea mariana (Mill.) Britt., Sterns & Pogg. (seedlings)
25. Geocaulon lividum (Richards) Fern.
26. Empetrum nigrum L.
27. Epilobium angustifolium L.
28. Arctostaphylos uva-ursi (L.) Spreng.
29. Ledum groenlandicum Oeder.
30. Vaccinium uliginosum L.
31. Vaccinium vitis-idaea L.



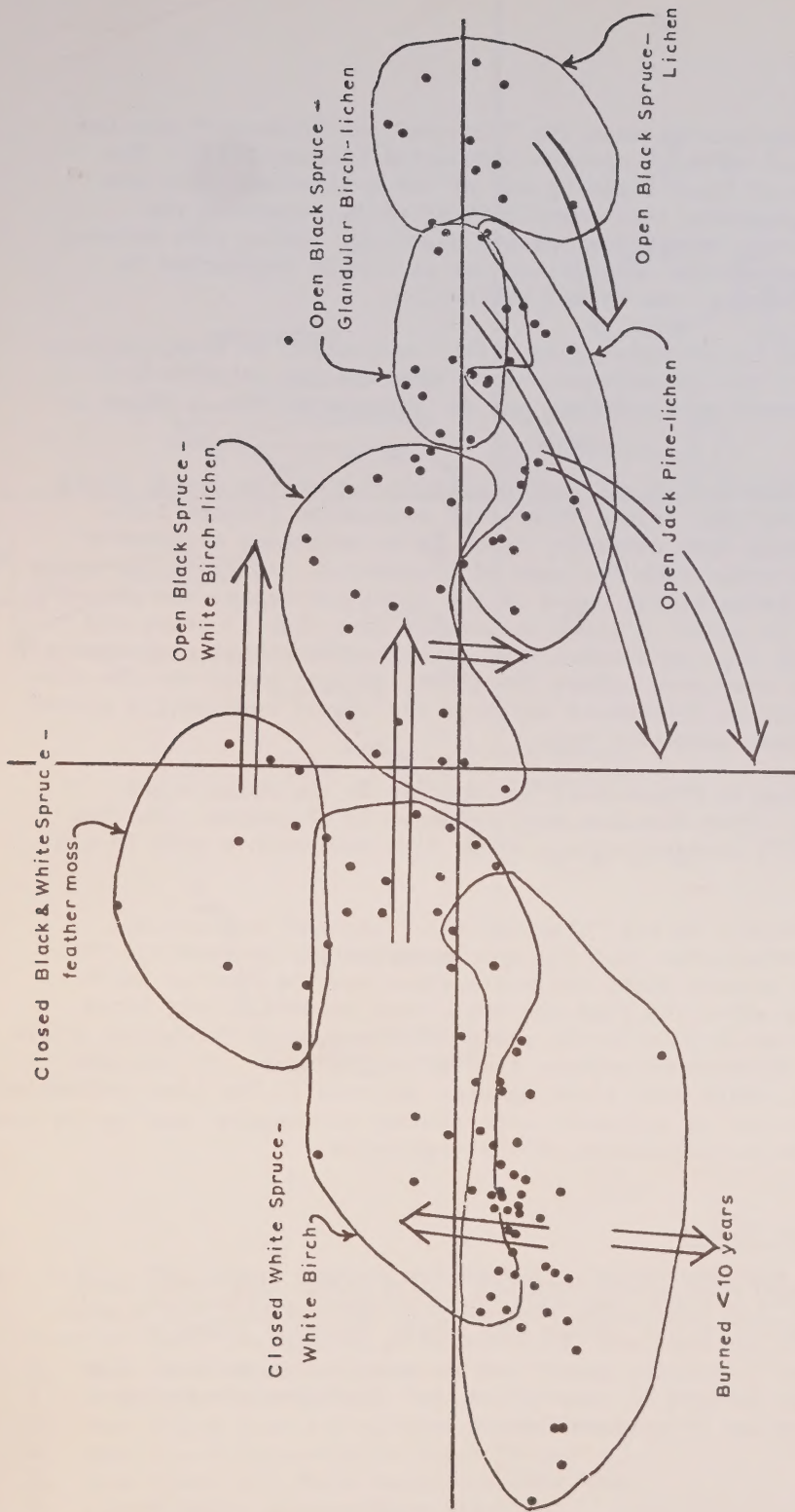


Figure 3.10 Schematic diagram showing changes from "time-out" to "time-in" ordination.

The difference between the "time-in" and "time-out" species ordinations gives a "time" species ordination (Figure 3.11). The method consists of first rotating one of the ordinations onto the other so as to maximize their similarities while retaining the invariance of their respective species loadings. Using this rotated solution the two species ordinations can be simply subtracted to give their difference, the "time" ordination.

In order to interpret this "time" ordination we have inserted into Figure 3.11 the chronosequences of some species in different community types. A more complete set of chronosequences is shown in Figure 3.12.

These chronosequences were constructed from the stands found in each community type in the "time-out" ordination (Figure 3.5). The classification into community types is an arbitrary means of dividing up the ordination for ease of discussion, the divisions along the ordination being mostly based on the prominent canopy and ground cover plants. In order to place the stands less than 10 years old into a community type we assumed that sites regenerate to approximately the composition they were before the fire. In most cases the pre-fire composition could be determined and thus the stands were easily placed in the appropriate community type.

Returning to Figure 3.11 the species on the upper right recover rapidly after fire but then decrease in abundance. Species on the lower left increase slowly after fire and reach a peak in old stands.

With respect to the "time-in" and "time-out" ordination, Figure 3.11 demonstrates that the species primarily responsible for the difference between these two ordinations are the species which recover rapidly after the fire and those that recover slowly after fire. Species which show little change with age after fire have little effect on the differences between the two ordinations. In the next section we will argue that these species patterns in the time ordination are characteristics of different life history strategies and can be used to explain changes in composition of the vegetation.

3.6 Species Change

The vegetation which occupies a site after fire comes from three sources: (1) vegetative reproduction (sprouting), (2) viable seeds buried in the soil and (3) invasion by propagules. Add to these the differences in species growth and recovery rates and much (but not all) of the changes in composition and abundance associated with succession can be rationalized.

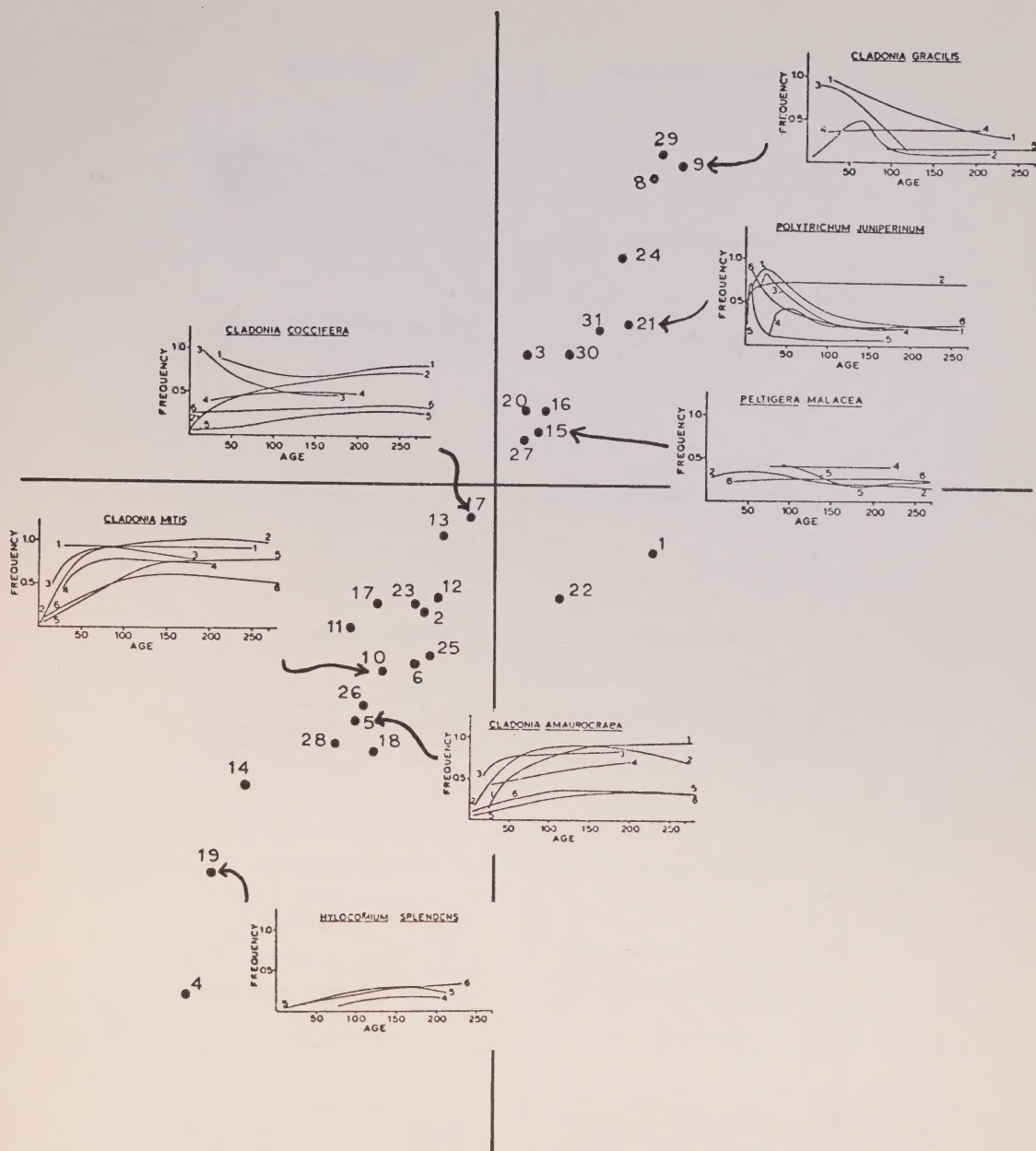


Fig. 3.11 The 'time' species ordination. Calculated from the difference between the 'time-in' and 'time-out' species ordination. Numbers on small recovery graphs correspond to the following community types:

1. Open Black Spruce-Lichen
2. Open Jack Pine-Lichen
3. Open Black Spruce-Glandular Birch-Lichen
4. Open Black Spruce-White Birch-Lichen
5. Open Black and White Spruce-Feather Moss
6. Closed White Spruce-White Birch

Numbers beside points correspond to species in Figure 3.4

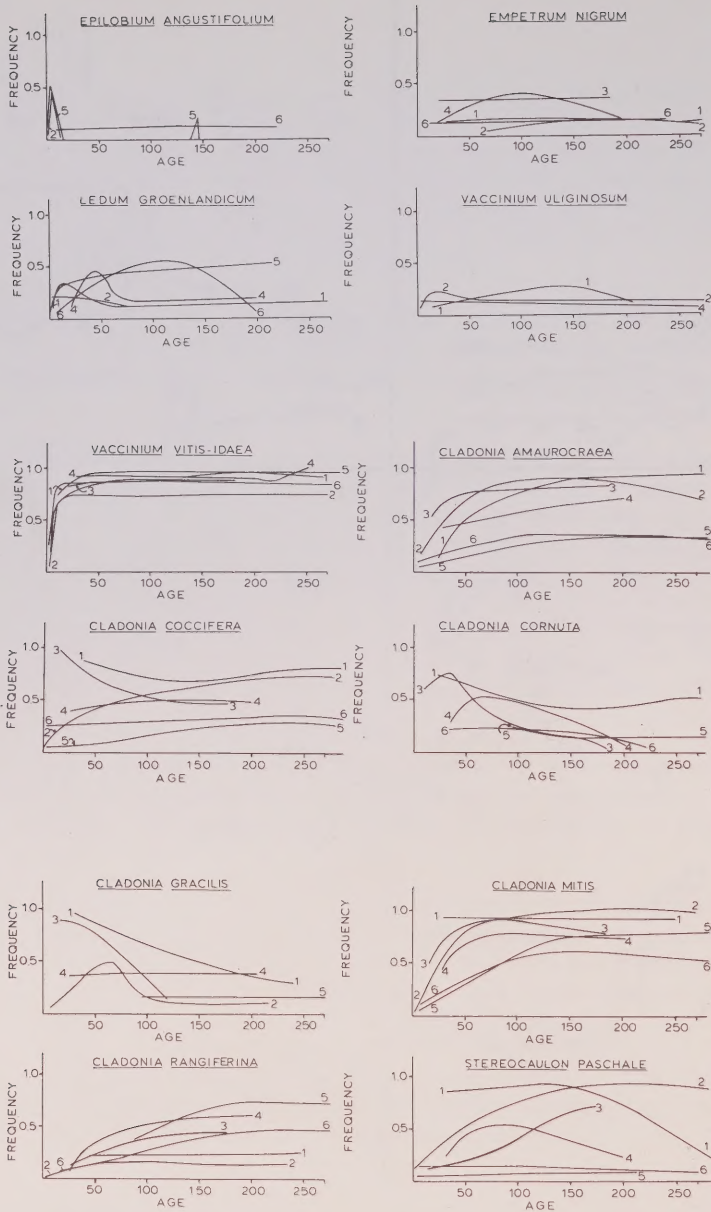


Fig. 3.12 Changes in species abundance in different community types. If a species has not been found in more than a few stands in one community type it was not plotted for that type.

1. Open Black Spruce-Lichen
2. Open Jack Pine-Lichen
3. Open Black Spruce-Glandular Birch-Lichen
4. Open Black Spruce-White Birch-Lichen
5. Closed Black and White Spruce-Feather Moss
6. Closed White Spruce-White Birch

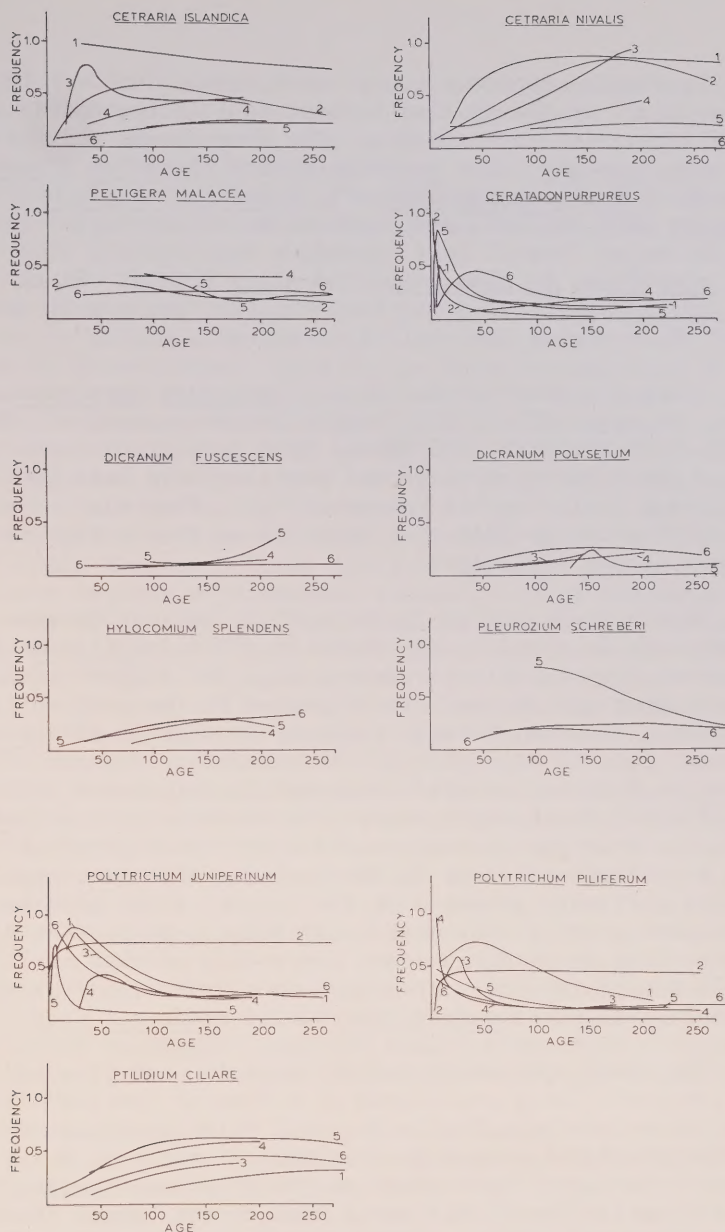


Fig. 3.12 Changes in species abundance in different community types. If a species has not been found in more than a few stands in one community type it was not plotted for that type.

1. Open Black Spruce-Lichen
2. Open Jack Pine-Lichen
3. Open Black Spruce-Glandular Birch-Lichen
4. Open Black Spruce-White Birch-Lichen
5. Closed Black and White Spruce-Feather Moss
6. Closed White Spruce-White Birch

Vegetative reproduction is most common in the woody shrubs in the subarctic. Of the species present in this region 81% have some means of vegetative reproduction. The four shrubs which occur in more stands than any other vascular plants (Empetrum nigrum 42% of the stands, Ledum groenlandicum 57%, Vaccinium uliginosum 43% and V. vitis-idaea 93%) all have efficient means of vegetative reproduction. Of the six major "trees" half reproduce vegetatively after fire—Betula papyrifera, B. glandulosa and Alnus crispa. Black spruce (Picea mariana) reproduces vegetatively but does not do so after fire. Pine and white spruce are strictly seeders.

Among the non-vascular plants Ceratodon purpureus and Polytrichum spp. are the most efficient at vegetative reproduction. These species show efficient sprouting and spread from underground stem bases or protonema after their above-ground portions have been destroyed or buried (Leach 1931, Marsh & Koerner 1972). They also have an ability to "conduct" water up from the substrate at fairly high soil water potentials (Bowen 1931, 1933).

Viable seeds buried in the soil in many ecosystems play an important role in speeding the recovery of the vegetation after disturbance; they quickly germinate, live for a short time, and produce another set of seeds to be buried in the soil until the next disturbance. However, buried viable seeds seem to play a relatively unimportant role in this part of the subarctic (Johnson 1975). No reproduction from buried seeds occurred in soil cores collected in the Caribou Range. Seeds were present in the soil but most proved to be non-viable. This almost complete lack of viable-germinable seeds is part of a northward decline in the buried viable seed populations which follow the northward decrease in the length of the growing season. The shortened growing season probably selects seeds that germinate rapidly as soon as conditions are favourable so that seedlings can make full use of the short growing season. Such a strategy may lead to the observed decrease in viable buried seeds.

The serotinous and retained cones of jack pine and black spruce are justifiably considered as a form of "buried" viable seeds. However unlike seeds buried in the soil which germinate on an environmental signal caused by disturbance (see e.g. Marks 1974) these two trees shed their seeds on the stimulus of heat from a forest fire which breaks the resin seal on the cones. Seeds are then shed onto the soil surface which probably is, after the fire, suitable for their germination. The control system operating in both buried seeds and serotinous cones is similar. Therefore the serotinous and retained cone habit of these trees make them very successful at reinvading burned stands. Only in exceptional cases is there a failure of regeneration of these species in stands within 5 years after fire.

Invasion by propagules seems to be the second most important means of reoccupation of burned sites. The speed of recovery of plants in this category depends on their rates of invasion and growth. Species such as Agrostis scabra, Carex spp., Calamagrostis spp., Corydalis spp., Epilobium spp. and Poa glauca which produce large numbers of light seeds are usually common right after fires.

Ground lichens seem to invade burns by small thallus fragments (see also Fink 1917, Ridley 1930). Their differences in recovery seem to be due to slight differences in invasion ability and larger differences in growth rate. This can be seen by comparing in Figure 3.12 the recovery rates of Cladonia mitis, a fast grower (Ahti 1959, Ahti & Hepburn 1967), with Cladonia rangiferina a slow grower.

Regional precipitation and habitat moisture regimes are important in understanding the drying of the lichen mat and in turn the assimilation and growth rate of lichens (Ahti 1959, Ahti & Hepburn 1967, Kershaw & Rouse 1971). Therefore relative differences in moisture regimes of different community types influence the rate of recovery of lichens and their maximum abundance. For example, Cladonia rangiferina (Figure 3.12) grows best in mesic environments which in our region, on upland sites, are closed spruce-feather moss sites. Furthermore the recovery rate and maximum abundance of C. rangiferina in different community types shows this moisture influence.

The abundance of some ground lichens, such as Stereocaulon paschale has been attributed to caribou grazing (Ahti & Hepburn 1967, Ritchie 1959, Scotter 1964). Unfortunately in the western subarctic direct observation of grazing effects are limited. It is our opinion that except in local habitats in late spring, little severe grazing occurs (see also Bergerud 1974, Miller 1972). It is therefore difficult to ascribe either the large areas covered with Stereocaulon paschale to heavy caribou grazing or the more limited areas covered with Cladonia alpestris and C. rangiferina to light caribou grazing. It is simpler to suggest that the behavior of these lichens is due primarily to their environmental requirements, particularly moisture.

An examination of the graphs in Figure 3.12 reveals a point essential to an understanding of temporal vegetation change, namely that in general most of the species that are found in older stands are present in the first years after fire (for similar results see Keever 1950, Egler 1954, Niering & Egler 1955, Hack & Goodlett 1960, Sigafos & Hendricks 1969, Ohmann & Ream 1971). However due to differences in growth rates species become prominent at different times in a stand's recovery. This is particularly obvious with the trees. For example on mesic sites where both white birch and black spruce make up the old forests, the density of black spruce is similar to white birch in these young stands, but birch is more prominent in the early years because it sprouts and grows faster than does

black spruce. A similar relationship exists on drier sites between jack pine and black spruce, where jack pine shows a faster growth rate and is more prominent in young stands. We do not mean to imply that there are no density changes with age but that there is little evidence of a compositional replacement series. Apparent exceptions to this rule are next discussed.

The feather mosses (Hylocomium splendens, Dicranum spp. Pleurozium schreberi) usually appear in stands 30 to 50 years after fire in mesic-higher nutrient habitats and quickly become the most abundant ground cover. Their occurrence in old, closed canopy, mesic stands which are rich in species has led many to the conclusion that these stands represent the climax stage. Hustich (1949) has stated the hypothesis clearly when he said "...if there is any such thing as climax forests in nature, the spruce-feather moss forest is certainly one of them".

However, another interpretation of the occurrence of feather mosses is possible. The closed canopy and species richness of these stands in which feather moss occurs can be explained by the better water and nutrient regimes of the sites due to their topographic positions, as already discussed in section 3.4. It is true that feather mosses are found only in older stands, but they do not necessarily occur in the oldest.

Tamm (1953, 1964) has shown that the feather-moss Hylocomium splendens' distribution is determined by the need for shade, moderate but abundant water and high nutrient levels. Feather mosses are not "rooted" in the substrate like Polytrichum and Ceratodon. Consequently, they are nearly independent of the substrate's nutrient and water supply. This explains why feather mosses quickly dry up and die when the canopy cover is not adequate to prevent high evaporation. Also because they absorb little or no nutrients from the substrate they are dependent on rain drip from the canopy for nutrients. Thus good site quality is necessary to assure a high nutrient level in the canopy foliage and a richer rain leachate for the moss on the ground to absorb. After fire, with canopy cover lacking, invasion by feather moss is prevented. Furthermore, the lack of attachment to the substrate prevents vegetative reproduction from surviving buried "stems", unlike such species as Polytrichum juniperinum.

However, given a shady, humid, high nutrient environment as is found in the cool, basal slopes of black and white spruce-feather moss stands, the feather mosses are very effective competitors against other species. They can quickly spread over and weaken or eliminate other ground plants such as lichens and haircap moss mats.

From this viewpoint, feather moss stands do not represent a climax in the sense of a stable terminal stage in a sequence of community replacement. Instead certain stands provide a habitat for

a group of mosses with "exacting" environmental specifications, i.e. a mesic, shady, high-nutrient environment. This environment occurs, but only on certain sites and then only after canopy closure at about 50 years. It is pertinent to note that feather mosses grow even in dry, nutrient-poor, open black spruce-lichen stands where suitable microhabitats exist in the shade of clones of birch or black spruce, where rain drip is enriched by canopy leachate. From either an ecological or geomorphological viewpoint it is unlikely that feather-moss stands will ever become widespread in this part of the subarctic.

3.7 Community Change

The speed of recovery after fire to a composition similar to that before the fire can be examined using the number of species (species richness) and percent canopy for stands of different ages. Figure 3.13 shows these changes with age for the six different community types.

The accumulation of species in the first 50 years after fire is approximately the same for all community types. However in mesic community types (e.g. closed black spruce and white spruce-feather moss) the species richness continues to increase after 50 years until the stands are approximately 100 years old or so. In some cases very old stands seem to show a slow decrease in species number although the number of old stands is so small that a firm conclusion cannot be reached. Examination of the data reveals that the increase in the number of species in young stands after fire is due primarily to vascular plants while in older stands the mosses and lichens account for the increase. This pattern is observable also in Figure 3.12.

Thus recovery of stands in terms simply of the number of species seems to indicate a remarkably similar pattern. This is because many species adapted to quick recovery are common to all sites. Recall that the early recovery of sites is primarily by vascular species and that four vascular shrubs are found in nearly all stands. The differentiation in species number in older stands is primarily due to differences in water, nutrients and energy budget, with mesic sites supporting more species than drier, poorer (in nutrients) sites.

The canopy cover shows a reestablishment pattern which is similar between community types. The pattern shows a rapid increase in cover up to about 50 years and then a decline. The degree of decline depends on the site, more mesic sites having much greater cover even at greater age than do drier, poor (in nutrients) sites. Examination of the information about pattern from the wandering quarter method shows the peak at 50 years is caused by the rapid sprouting and growth of birch (Betula papyrifera). This gives young stands their

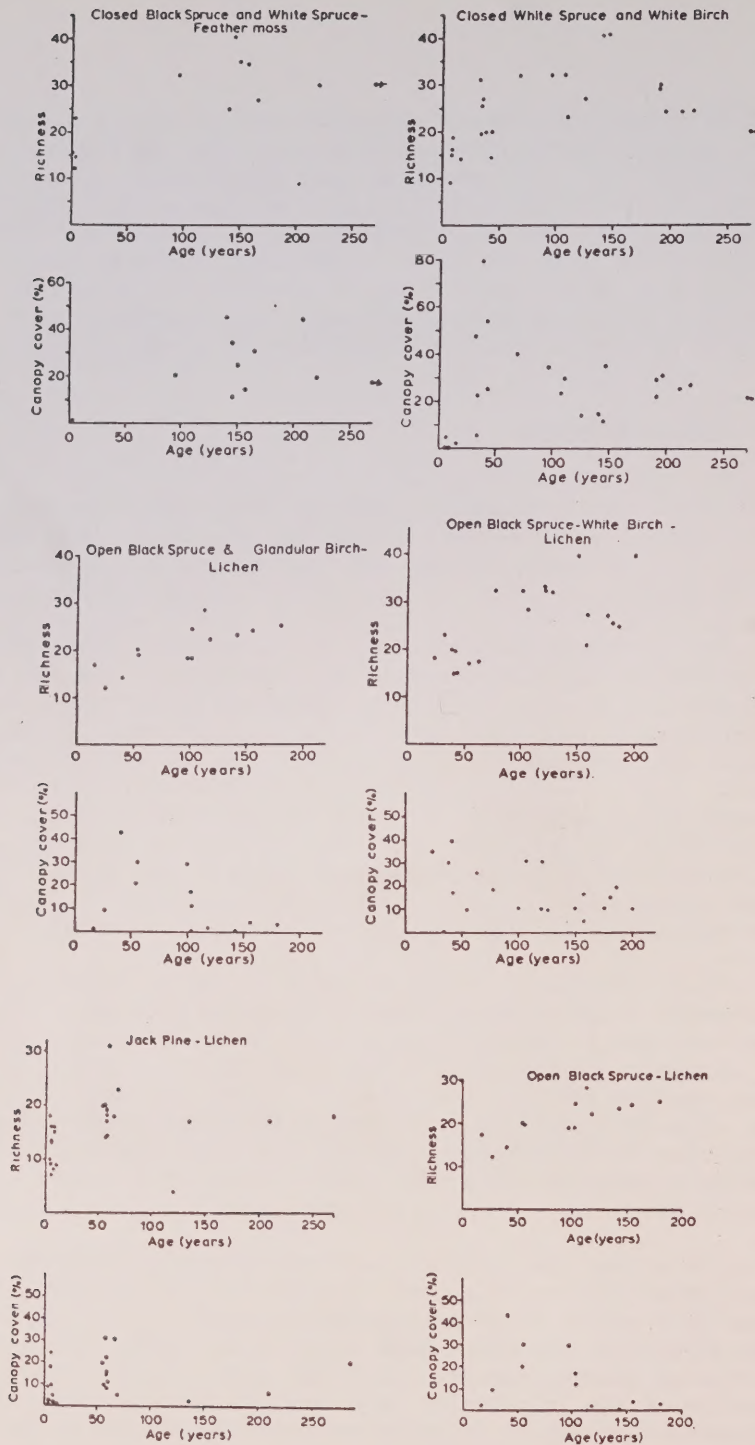


Figure 3.13 Changes in species number (richness) and canopy cover with age for different community types.

characteristic light green colour. After about 50 years these clones begin to senesce, opening up the stands. In certain stands however birch are always present and it is not surprising to find white birch of 120 or more years old.

3.8 Discussion

In the following paragraphs we will briefly outline our understanding of vegetation compositional change in both space and time. Plants which sprout quickly regain their pre-fire level of abundance. In some cases, because of the reduced competition and/or increased availability of nutrients, they may actually increase in abundance above their pre-fire level for a while. Such species will be found in most stands until the next fire because of their long life spans and relatively good competitive abilities.

Between the sprouting perennial species, areas are open to colonization. In older stands these spaces are filled with lichens and a few herbaceous and woody species. Plants that produce abundant, light seeds (e.g. Epilobium spp. and Corydalis spp.) invade this open habitat early. These species have fast growth rates. They mature, flower, fruit and die out or are greatly reduced in number after 5 to 10 years. As a group these species can stand little competition and thus are present only for the brief low competition (and high nutrient) period right after fire. They are often called fugitive species (cf. Hutchinson 1953) because as a population they "move around" to find low competition sites by producing large numbers of light seeds. Once established they grow rapidly, flower quickly and produce large numbers of light seeds enabling them to escape (as a population) the site before the competition becomes too great. Many of these species, e.g. Epilobium angustifolium prefer sites with high nitrate, the soil nutrient which usually signals disturbance.

The species which are common in older stands also invade early in most cases but have slower growth rates and so may not appear as abundant as other faster growing species. The older stands show species with life histories which have many similarities—slower growth, delayed first reproduction, fewer and heavier seeds, longer lives. The vegetation composition has changed in that most of the fugitive species have become extinct because of their short life span and the increasing competition. The survivors are those that live long and are able to retain a place in a now crowded habitat.

From this viewpoint, change in vegetation composition is a result of different strategies of life history of species adapted to particular habitats. Recently burned stands have a predominance of quickly invading, rapidly growing, short-lived fugitive species in a matrix of slower invading, slow growing, long lived species. The

exact balance of different kinds of life histories depends on the frequency of disturbance and the severity of the site. In regions of frequent disturbance and/or high stress, "older" stands will have more short lived, fast growing species adapted to lower competitive stress and will thus appear to be more of a "pioneer" type. On the other hand in regions of infrequent disturbance and/or low stress, "older" stands will have long lived, slow growing, highly competitive species and will appear to be more of a "mature" type.

For the land manager our results should indicate that fire is a natural and integral part of the subarctic ecosystem. The adaptation of this ecosystem to disturbance by fire is demonstrated in the combination of species of different life histories. This combination of life histories allows a flexible response on the part of the ecosystem to different frequencies and intensities of fire.

We must learn to see the subarctic ecosystems not as a succession of communities as shown in Figure 3.1, in which the trend is from an unstable to a stable, climax stage but instead, as a system in which each part of the recovery after fire is in a steady state.

4. REFERENCES

- Ahti, T. 1959. Studies on the caribou lichen stands of Newfoundland. *Annales Bot. Soc. Zool.-Bot. Fenn.* 'Vanamo', 30: 1-43.
- Ahti, T. and R.L. Hepburn. 1967. Preliminary studies on woodland caribou range, especially on lichen stands, in Ontario. *Dep. Lands Forests, Ont. Res. Rep. Wildlife No. 74*, 134 p.
- Argus, G.W. 1966. Botanical Investigations in Northeastern Saskatchewan: the subarctic Patterson-Hasbala Lakes region. *Can. Field Nat.* 80: 119-143.
- Barney, R.J. 1971. Selected 1966-69 interior Alaska wildfire statistics with long term comparisons. U.S. Dept. Agriculture Forest Service PNW-154. 13 p.
- Barry, R.G. 1967. Seasonal location of the arctic forest over North America. *Geogr. Bull. (Canada)* 9: 153-206.
- Batcheler, C.L. 1971. Estimation of density from a sample of joint point and nearest-neighbor distances. *Ecology* 52: 703-709.
- Bergerud, A.T. 1974. Relative abundance of food in winter for Newfoundland caribou. *Oikos* 25: 379-387.
- Bowen, E.J. 1931. Water conduction in Polytrichum commune. *Ann. Bot. (Lond)* 45: 175-200.
- Bowen, E.J. 1933. The mechanism of water conduction in the Musci considered in relation to habitat. *Ann. Bot. (Lond)* 47: 401-422, 635-661, 889-912.
- Brown, W.G.E. 1961. The caribou winter range vegetation in the Stony Rapids Area, Saskatchewan. Unpublished report. Canadian Wildlife Service, CWS 234, Ottawa. 14 p.
- Bryson, R.A. 1966. Air masses, streamlines and the boreal forest. *Geogr. Bull. (Canada)* 8: 228-269.
- Buffo, J., L.J. Fritschen and J.L. Murphy. 1972. Direct solar radiation on various slopes from 0 to 60° north latitude. U.S. Dept. Agriculture Forest Service PNW-142. 74 p.
- Byran, G.M. and G.M. Jemison. 1943. Solar radiation and forest fuel moisture. *J. Agric. Res.* 67: 149-176.
- Camsell, C. 1916. An exploration of the Tazin and Taltson Rivers, Northwest Territories. *Geol. Soc. Canada, Memoir No. 84*.

- Catana, H.J. 1963. The wandering quarter method of estimating population density. *Ecology* 44: 349-360.
- Craig, B.G. 1964. Surficial geology of east-central District of Mackenzie. *Geol. Soc. Canada Bull.* No. 99.
- D'Agostino, R.B. 1971. Linear estimation of the Weibull parameters. *Technometrics* 13: 171-182.
- Dix, R.L. and J.M.A. Swan. 1971. The role of disturbance and succession in upland and forest at Candle Lake, Saskatchewan. *Can. J. Bot.* 49: 657-676.
- Drury, W.H. and I.C.T. Nisbet. 1973. Succession. *J. Arnold Arbor.* 54: 331-368.
- Egler, F.E. 1954. Vegetation science concepts. I. Initial floristic composition—a factor in old field vegetation development. *Vegetatio* 4: 412-417.
- Fink, B. 1917. The rate of growth and ecesis in lichens. *Mycologia* 9: 138-158.
- Frissel, S.S., Jr. 1973. The importance of fire as a natural ecological factor in Itasca State Park, Minnesota. *Quaternary Res.* 3: 397-407.
- Furnival, G.M., W.E. Reifsynder, E. Wyler and T.G. Siccama. 1969. Solar climate calculator. Third Forest Microclimate Symp. Proc. p. 181-187. Kanaskis Forest Exp. Sta., Seebee, Alberta.
- Geiger, R. 1965. The climate near the ground. Cambridge, Mass: Harvard Univ. Press. 611 p.
- Hack, J.T. and J.C. Goodlett. 1960. Geomorphology and forest ecology of a mountain region in the central Appalachians. U.S. Geol. Surv. Prof. Paper 347. 64 p.
- Hare, F.K. 1950. Climate and zonal divisions of the boreal forest formation in eastern Canada. *Geogr. Rev.* 40: 615-635.
- Harter, H.L. and A.H. Moore. 1965. Maximum-Likelihood estimation of the parameters of Gamma and Weibull populations from complete and from censored samples. *Technometrics* 7: 639-643.
- Hayes, G.L. 1941. Influence of altitude and aspect on daily variations in factors of forest-fire danger. U.S. Dept. Agric. Circular No. 591. 38 p.
- Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Water Canoe Area, Minnesota. *Quaternary Res.* 3: 329-382.

- Henry, J.D. and J.M.A. Swan. 1974. Reconstructing forest history from live and dead plant materials—~~an approach to the study of forest succession in southwest New Hampshire.~~ Ecology 55: 772-783.
- Hoadley, J.W. 1955. Abitau Lake, District of Mackenzie, Northwest Territories. Geol. Soc. Canada Paper 55-10.
- Hobson, R.D. 1967. Fortran IV programs to determine surface roughness in topography for the CED 3400 computer. Kansas Computer Contribution No. 14. 28 p.
- Hobson, R.D. 1972. Surface roughness in topography: quantitative approach. in R.J. Chorley (ed.). Spatial Analysis in Geomorphology. New York: Harper and Row Pub.
- Houston, D.B. 1973. Wildfire in northern Yellowstone National Park. Ecology 54: 1111-1117.
- Hustich, I. 1949. On the forest geography of the Labrador Peninsula: a preliminary synthesis. Acta. Geogr. 10: 1-63.
- Hutchinson, G.E. 1953. Copepodology for the ornithologist. Ecology 32: 571-577.
- Johnson, E.A. 1975. The buried seed populations in the subarctic forest east of Great Slave Lake, N.W.T. Can. J. Bot. 53: 2933-2941.
- Johnson, E.A. 1976. Climatic effects on forest fire occurrence in the Mackenzie District, N.W.T. Manuscript.
- Johnson, E.A. and J.S. Rowe. 1975. Fire in the wintering grounds of the Beverley caribou herd. Amer. Midl. Nat. 94: 1-14.
- Keever, C. 1950. Causes of succession on old fields of the Piedmont, North Carolina. Ecol. Monogr. 20: 229-250.
- Kelsall, J.P., E. Kuyt and S. Zoltai. 1971. Ecology of the Ft. Reliance - Artillery Lake area. Report prepared by the Can. Wildl. Serv. for the Parks Branch, Dept. Indian and Nor. Aff. 99 p.
- Kendall, G.R. and A.G. Petrie. 1962. The frequency of thunderstorm days in Canada. Meteor. Br. Dept. Transport CIR 3688, TEC-418. 17 p.
- Kershaw, K.A. and W.R. Rouse. 1971. Studies on lichen-dominated systems. II. The growth pattern of Cladonia alpestris and Cladonia rangiferina. Can. J. Bot. 49: 1401-1410.
- Kershaw, K.A., W.R. Rouse and B.T. Bunting. 1975. The impact of fire on forest and tundra ecosystems. ALUR 74-75-63, Arctic Land Use Research Program, Dept. Indian and Northern Affairs. Information Canada. 81 p.

- Kiil, A.D. 1971. A statistical summary of forest fires in the Yukon Territory. 1966-1969. Canadian For. Serv. Information Report NDR-X-10. 21 p.
- Larsen, J.A. 1965. The vegetation of the Ennadai Lake Area, N.W.T. Ecol. Monogr. 35: 37-59.
- Larsen, J.A. 1971. Vegetation of Fort Reliance, N.W.T. Can. Field-Nat. 85: 147-178.
- Leach, W. 1931. On the importance of some mosses as pioneers on unstable soils. J. Ecol. 19: 98-102.
- Maini, J.S. 1966. Phytoecological study of sylvo-tundra at Small Tree Lake, N.W.T. Arctic 19: 220-243.
- Marks, P.L. 1974. The role of pin cherry (Prunus pensylvania L.) in the maintenance of stability in northern hardwood ecosystem. Ecol. Monogr. 44: 73-88.
- Marsh, W.M. and J.M. Koerner. 1972. Role of moss in slope formation. Ecology 53: 489-493.
- Miller, D. 1972. Feeding behavior of barren-ground caribou on taiga winter ranges. Internat. Conf. on the behavior of ungulates in relationship to Manage. Calgary, Alberta.
- Menon, M.V. 1963. Estimation of the shape and scale parameters of the Weibull distribution. Technometrics 5: 175-182.
- Mitchell, V.L. 1973. A theoretical tree line in central Canada. Ann. Assoc. Amer. Geogr. 63: 296-301.
- Niering, W.A. and F.E. Egler. 1955. A shrub community of Viburnum lintago stable for twenty-five years. Ecology 36: 356-360.
- Ohmann, L.F. and R.R. Ream. 1971. Wilderness ecology: virgin plant communities of the Boundary Waters Canoe Area. U.S. Dept. Agriculture. Forest Service NC-63. 55 p.
- Raup, H.M. 1930. The vegetation of the Fort Reliance sand plain. Ann. Carnegie Mus. 20: 9-38.
- Raup, H.M. 1964. Some problem in ecological theory and their relation to conservation. J. Ecol. 52 (Suppl.): 19-28.
- Requa, L.E. 1964. Lightning behavior in the Yukon. Proc. Ann. Tall Timbers Fire Ecol. Conf. 3: 111-119.
- Ridley, H.N. 1930. The dispersal of plants throughout the world. Ashford, Kent: L. Reeve and Co. Ltd. 744 p.

- Ritchie, J.C. 1958. A vegetation map from the southern spruce forest zone of Manitoba. *Geographical Bull. (Canada)* 12: 39-46.
- Ritchie, J.C. 1959. The Vegetation of N. Man. III. Studies in the Subarctic. *Arctic Institute of North America. Tech. Paper No. 3*, 56 p.
- Rouse, W.R. and K.A. Kershaw. 1971. The effects of burning on the heat and water regimes of lichen-dominated subarctic surfaces. *Arctic and Alpine Research*, Vol. 3, No. 4, 1971, p. 291-304.
- Rowe, J.S. 1970. Spruce and fire in northwest Canada and Alaska. *Proc. Ann. Tall Timbers Fire Ecol. Conf.* 10: 245-254.
- Rowe, J.S. 1972. Forest Regions of Canada. *Dept. of Environ., Can. For. Serv. Publication No. 1300*.
- Rowe, J.S., J.L. Bergsteinsson, G.A. Padbury and R. Hermesh. 1974. Fire Studies in the Mackenzie Valley. ALUR 73-74-61, Arctic Land Use Research Program, Dept. Indian and Northern Affairs. *Information Canada*. 123 p.
- Rowe, J.S. and E.A. Johnson. 1974. Problem analysis and pilot studies of fire in the western subarctic with particular reference to the Caribou Range, N.W.T. A report prepared for Canadian Forestry Service and Canadian Wildlife Service. 89 p.
- Rowe, J.S., D. Spittlehouse, E. Johnson and M. Jasieniuk. 1975. Fire studies in the upper Mackenzie Valley and adjacent precambrian uplands. ALUR 74-75-61, Arctic Land Use Research Program, Dept. Indian and Northern Affairs. *Information Canada*. 128 p.
- Scotter, G.W. 1964. Effects of Forest Fires on the Winter Range of Barren Ground Caribou in Northern Saskatchewan. *Can. Wildlife Serv., Wildl. Manage. Bull., Ser. 1 No. 18*. Northern Affairs and National Resources. 111 p.
- Scotter, G.W. 1965. Study of the winter range of the barren-ground caribou with special reference to the effects of Forest Fires. Progress report No. 3. Unpublished report CWS 1129.
- Scotter, G. 1968. Effects of forest fires on the lichen winter ranges of barren-ground caribou in northern Canada. Ph.D. thesis Utah State Univ. 65 p.
- Sigafoos, R.S. and E.L. Hendricks. 1969. The time interval between stabilization of alpine glacial deposits and establishment of tree seedlings. *U.S. Geol. Survey Prof. Paper 650-B*: 89-93.
- Simard, A.J. 1974. Forest fire weather zones of Canada. *Can. Forest Service, Environment Canada*.

- Sokal, R.R. and F.J. Rohlf. 1969. Biometry. San Francisco: W.H. Freeman and Co. 776 p.
- Tamm, C.O. 1953. Growth, yield and nutrition in carpets of a forest moss (Hylocomium splendens). Meddel. Fran Statens Skogsforskningsinst. (Stockholm) 43: 1-140.
- Tamm, C.O. 1964. Growth of Hylocomium splendens in relation to tree canopy. Bryologist 67: 423-426.
- Taylor, F.C. 1956. Hill Island Lake (East half), District of Mackenzie, Northwest Territories. Geol. Soc. Canada Paper 55-16.
- Taylor, F.C. 1959. Nonacho Lake, Northwest Territories. Geol. Soc. Canada Map 10-1959.
- Van Wagner, C.E. 1974. Structure of the Canadian forest fire weather index. Can. For. Ser. Pub. No. 1333, 44 p.
- Vogl, R.J. 1970. Fire and the northern Wisconsin pine barrens. Proc. Ann. Tall Timber Fire Ecology Conf. 10: 175-209.
- Weibull, W. 1951. A statistical distribution function of wide applicability. J. of App. Mech. 18: 293-297.
- Whittaker, R.H. 1957. Recent evolution of ecological concepts in relation to the eastern forests of North America. Amer. J. Bot. 44: 197-206.
- Wright, G.M. 1951. Preliminary map, Christie Bay, Northwest Territories. Geol. Soc. Canada Paper 51-25.
- Wright, G.M. 1967. Geology of the southeastern Barren Grounds, Parts of the Districts of Mackenzie and Keewatin. Geol. Soc. Canada, Memoir No. 350.
- Wright, H.E. 1974. Landscape development, forest fires, and wilderness management. Science 186: 487-494.

CAI IA 77A61

Canada. DINA.

ALUR 75-76-61

FIRE AND VEGETATION CHANGE IN THE WESTERN SUBARCTIC
1977.

**RESOURCE CENTRE
INST. FOR ENVIORN'L. STUDIES
UNIVERSITY OF TORONTO**



